The Pliocene flora of Frankfurt am Main, Germany: taxonomy, palaeoenvironments and biogeographic affinities

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Abstract

The Pliocene flora of Frankfurt am Main described by Karl Mädlér during the first half of the twentieth century is a key flora for the European Pliocene. In the present study, we revised the leaf fossil taxa described by Mädlér and investigated plant material collected after Mädlér's publication. The revised and augmented floral list comprises seven new species and some new combinations of taxa described by Mädlér. In total, 16 gymnosperm species in 15 genera and 73 angiosperm species (of which 15 could not be assigned to a genus) in 40 genera are recognised in the leaf record. Main characteristics of the flora are the high diversity of conifers, the diverse assemblage of exclusively deciduous Fagaceae, including six species of oaks, and the high diversity of Rosaceae. These features indicate cool temperate climatic conditions (comparable to Lugano in southern Switzerland). Angiosperm genera that are today confined to North America and/or East Asia (*Eucommia*, *Magnolia* and *Sassafras*) also are deciduous, whereas evergreen taxa are shrubs typical of the understorey (*Buxus*, *Ilex*, *Pachysandra*, *Prunus lusitanica* type) and *Viscum*. Eighteen taxa recorded in the Pliocene of Frankfurt am Main are today absent from western Eurasia and eastern North America, and 25 taxa are absent from western North America. This shows (i) a strong biogeographic link of the Pliocene flora of Frankfurt am Main with East Asia, (ii) surprisingly high levels of speciation (Pliocene endemisms) and (iii) that the European flora was more diverse in woody species shortly before the onset of major Pleistocene glaciations than today.

Keywords Flora · Relict taxa · Speciation · Biogeography · Pliocene · Europe

Introduction

Global cooling after the warm and mild phases of the Miocene (Zachos et al. 2001) led to a modernisation of north temperate

floras (Mai 1995). The early part of the Pliocene (5.3–3.6 Ma) was characterised by warm conditions (ca. 3 °C higher global surface temperatures) and higher sea levels (10–20 m; Ravelo et al. 2004) and slightly higher CO₂ concentrations (Beerling and Royer 2011). During the second part of the Pliocene, gradual cooling culminated in a significant intensification of northern hemispheric glaciation at ca. 2.75 Ma (Ravelo et al. 2004). Despite this, many exotic taxa persisted as relicts from older epochs (Mai 1995; Martinetto 2001), and modern diversity patterns of woody species (trees and shrubs) across the Northern Hemisphere were established only during and after the major Pleistocene glaciations (Magri et al. 2017). Today, species of the north temperate forest flora are distributed among western Eurasia, East Asia, western North America and eastern North America, approximately in the ratio 2:12:1:4 (Latham and Ricklefs 1993). These figures illustrate the strongly impoverished postglacial flora of Europe.

The Pliocene flora of Frankfurt am Main, Hessen, Germany (hereafter Frankfurt/M., Fig. 1), is a key flora for the European Pliocene. This flora has been repeatedly described (e.g. Geyler

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Fig. 1 Location of the studied flora of Frankfurt/Main (a) and position of the “Klärbecken Flora” site in Niederrad within Frankfurt/M. (b)

and Kinkelin 1887; Engelhardt and Kinkelin 1908; Mädler 1939) and is one of the richest macrofloras in the European Pliocene (Mai 1995). After Mädler’s monograph, the Frankfurt “Klärbecken Flora” has never been revised.

After a previous revision of the Pliocene leaf flora of Auenheim, France (Kvaček et al. 2008), the main objectives of the present study were to re-assess previously published leaf morphotypes and to describe unpublished plant material of the Pliocene “Klärbecken Flora” site in Niederrad, Frankfurt/M. A major problem for the revision of this flora was that most of the material gathered since 1885 and housed at the Senckenberg Research Institute and Natural History Museum Frankfurt as a unique “glass herbarium” (Kräusel 1940) was destroyed in 1945 during World War II (Schaarschmidt 1980). Therefore, our objectives were (i) to investigate duplicate material, which could serve as a basis for the re-assessment of the Pliocene flora of Frankfurt (Mädler 1939), and (ii) to describe additional unpublished material recovered after World War II (Schaarschmidt 1980). Duplicates and unpublished material are housed in the collections of the Senckenberg Research Institute and Natural History Museum Frankfurt, Swedish Museum of Natural History, Stockholm and British Museum of Natural History, London Natural Science museum. Only leaf fossils are dealt with in this review, while the wood and palaeocarpological records (Supplementary material File 1) are left aside for future studies. The revised plant material was

then used to assess biogeographic relationships of the flora of Frankfurt and to evaluate speciation events in the Pliocene. Finally, some conclusions regarding palaeoenvironments and palaeoclimate are presented.

Material and methods

Duplicate material and unpublished material of the Pliocene flora of Frankfurt

When studying the collections at the Senckenberg Research Institute and Natural History Museum Frankfurt, one of us (Z.K.) noticed a sheet of paper with a list of material sent to the “Naturhistorisches Reichsmuseum Stockholm”, written by an anonymous keeper and without an author and date with a mechanical typewriter and containing out-of-date taxonomy (e.g. *Planera ungeri*). This short text lists *Ginkgo adiantoides* (leaf fragments), *Abies pectinata* (one seed cone), *Picea latisquamosa* (seed cone), *Pinus montana fossilis* (one seed cone), *Pinus timleri* (seed cone scale), *Acer* sp. (fruits), *Betula* (fruit bracts), *Buxus sempervirens* (leaves and fruit cupules), *Carpinus grandis* (leaf, involucre fragment), *Carya alba fossilis* (fruits), *Carya ovata* (fruits), *Corylus avellana* (fruits), *Fagus pliocaenica* (leaves), *Ilex aquifolium* (leaf remains), *Juglans cinerea fossilis* (fruits), *Liquidambar pliocaenicum* (infructescences), *Planera*

ungeri (leaves) and *Quercus* (one leaf fragment). Additional notes on this sheet are written by hand and dispatched on the 19th February 1939 with a note that particularly conifer material would be welcome. Additions include *Torreya nucifera fossilis* (one fragmentary needle and epidermal preparation), *Podocarpus kinkelinii* (three leaves in one preparation), *Abies pectinata fossilis* (needle), *Abies sclereidea* (two needle fragments), *Sequoia langsdorfii* (three preparations), *Taxodium distichum fossilis* (one preparation), *Libocedrus pliozänica* (one twig), *Carya globosa* (one stone), *Viscophyllum pliozanicum* (leaf and epidermal preparation), *Styrax obovatum* (two stones), *Stuartia europaea* (one fruitlet) and *Buxus sempervirens fossilis* (one epidermal preparation). Further, material of *Pinus timleri* (two seeds), *Viscophyllum miquelii* (one leaf and one epidermal preparation) and *Ilex aquifolium fossilis* (one leaf and an epidermal preparation) was also sent to Stockholm. Hence, for the present re-assessment, we also concentrated on the material stored at the Stockholm museum (see [Supplementary material File 1](#) for carpological material housed at the Stockholm museum).

Duplicates of the original or additional specimens from the Pliocene flora of Frankfurt/M. are likely to be found in more institutions. We have seen additional material at the British Museum of Natural History, London, distributed by Richard Kräusel. Such glass preparations and slabs with macrofossils are the only remnants of the once very rich collections of the Pliocene plant assemblage of Frankfurt that had been assembled since 1884 and were mainly known as “glass herbarium” (Kräusel 1939).

Five papers dealing with material from the Pliocene of Frankfurt, namely on leaves of *Fagus* (Kvaček and Walther 1991; Denk 2004), seed cones of *Pinus timleri* (Kvaček et al. 2014a, b), *Pseudotsuga loehrii* (Kunzmann 2014), and leaves of *Ginkgo* (Denk and Velitzelos 2002) have been published after the classical paper by Mädlar (1939); they are considered in the systematic part.

Preparation of the fossil material

The preparations of leaf fossils that formed the basis of the previous studies of the Pliocene flora of Frankfurt/M. followed a protocol described in Mädlar (1939, p. 6). The sandy layers included “leaf beds”, which allowed, after soaking in water and KOH, a mechanical separation of leaf fossils. The first extensive work of preparing slide preparations of fossil leaves was done by F. Kinkel in (Mädlar 1939). The mummified leaf fossils were embedded between glass frames of the same size in glycerol and sealed with an unknown material. This procedure turned out to be less successful because glycerol evaporated through the framing. Later, Mädlar attempted to improve the collection by spreading leaf fossils on glass, embedded in glycerol jelly and covered by a smaller plastic sheet, then sealed with Canada balsam (Mädlar 1939, pp. 5–6).

Unfortunately, most of these glass preparations were destroyed as mentioned above. The procedure developed by Mädlar was also employed for preparations of the newly excavated material obtained by Richard Kräusel who transferred it for further preparation work to Wolfgang Haas in 1956 (see personal letter by Kräusel to Haas in the archive of the Department of Palaeobotany of the Senckenberg Museum; Volker Wilde, personal communication 2014). These specimens are quite well preserved and used in the present study. Only in rare cases the embedding material (glycerol jelly) partly dried out.

The collection of new preparations is now housed in the Section of Palaeobotany, Senckenberg Research Institute and Natural History Museum Frankfurt. It is arranged systematically according to the fossil species. The inventory numbers (SF.B numbers) follow this systematic arrangement. The numbers were scratched onto the glass slides by an anonymous keeper.

For the present study, only a small part of the glass preparations of macrofossils has been re-opened to get leaf lamina fragments for cuticle preparations. Mädlar (1939) used Schulze solution in combination with ammonia for maceration and a similar method was employed for the present study except for using 5% KOH instead of ammonia (see protocol in Kvaček et al. 2008). The preparation of cuticles was not always successful, namely in case of delicate cuticles of deciduous foliage when highly diluted Schulze reagent was used for maceration. Although not attempted here, fluorescence microscopy may turn out to be promising in future research.

The newly revised specimens and epidermal slides are housed in the collection of the Senckenberg Research Institute and Natural History Museum Frankfurt (numbers with prefix SF.B). Some specimens of the original material available for this study are housed at the Swedish Museum of Natural History, Stockholm (numbers starting with S) and the British Museum of Natural History, London (specimens numbered with prefix V).

Inferring palaeoclimate and palaeoenvironments

Palaeoclimate and palaeoenvironment estimates were made using Climate Leaf Analysis Multivariate Program (CLAMP) and Integrated Plant Record (IPR) vegetation analysis. The CLAMP method (e.g. Wolfe and Spicer 1999) uses physiognomic characteristics of the studied plant assemblage of Frankfurt/Main presented in [Supplementary material File 2](#) and the physiognomic and gridded meteorological calibration datasets from 144 sites “Physg3br/GRIDMet3br” (see Spicer et al. 2009) selected by the statistical tool published by Teodoridis et al. (2012). The CLAMP analysis was performed using a web application designed by Yang et al. (2011), which is free to access at the official CLAMP website (Spicer 2011–2019; for details, see [Supplementary material File 2](#)).

The IPR-vegetation analysis is a semi-quantitative method (Kovar-Eder et al. 2008) to evaluate zonal vegetation. This

method scores key component groups (functional types) of the integrated plant fossil record. This technique has been verified using modern plant assemblages from SE China and Japan (Teodoridis et al. 2011) and has recently been tested by the second author using living European and Caucasian plant assemblages (Bohn et al. 2004).

Systematic palaeobotany

The leaf taxa listed below were partly described by Karl Mädlar in his original study (Mädlar 1939) and were dealt with by various authors in subsequent studies (mentioned in the synonymies). Several novelties for the Pliocene flora of Frankfurt/M. have been provisionally indicated in the collections (possibly by R. Kräusel); other undescribed taxa are here suggested for the first time. Only a few separate papers have appeared recently, which are related to the Pliocene flora of Frankfurt/M. (e.g. Kvaček and Walther 1991; Denk 2004), partly based on the material from other sites (e.g. *Pinus timleri* by Kvaček et al. 2014a, b; *Ilex geissertii* by Kvaček et al. 2008). We prefer to assign the fossils to fossil-species instead of using names of modern taxa followed by “*fossilis*” as Mädlar (1939) did. This usage is still maintained in current papers dealing with Pliocene taxa (e.g. Geissert 1973; Mai and Walther 1988; Hably and Kvaček 1997; Knobloch 1998). In a few cases, when leaf morphology and cuticle structure are virtually identical with modern species, e.g. *Acer platanoides*, we called the fossil-taxon *Acer* aff. *platanoides*, indicating that the fossil most likely represents the lineage leading to the modern species, but perhaps not the species itself.

The arrangement of taxa follows the system based on the classification suggested by the Angiosperm Phylogeny Group (APG IV 2016). The collections studied include also fossils of reproductive organs (seed cones, winged carpological material), which are briefly mentioned in the systematic section but not treated in detail. Only selected foliage specimens of the entire collection are listed and illustrated, mainly those studied by epidermal anatomy. Descriptions are only provided for taxa that have not been described by Mädlar (1939).

Gymnosperms
Ginkgoaceae Engler
Ginkgo Linnaeus

Ginkgo adiantoides (Unger) Heer
Fig. 2a–c

1939 *Ginkgo adiantoides* (Unger) Heer; Mädlar, p. 46, pl. 5, figs. 1–4

Fig. 2 **a** *Ginkgo adiantoides* (Unger) Heer, leaf, SF.B 11495a, 10 mm. **b** *Ginkgo adiantoides* (Unger) Heer, leaf, SF.B 11495b, 10 mm. **c** *Ginkgo adiantoides* (Unger) Heer, leaf, SF.B 11493, 10 mm. **d** *Calocedrus pliocaenica* (Kinkelin) Kvaček, Teodoridis et Denk comb. nov., needle leaf, neotype S082691, 10 mm. **e** *Glyptostrobus europaeus* (Brongniart) Unger, leafy shoot, V 17167, 10 mm. **f** *Sequoia abietina* (Brongniart) Erw. Knobloch, leafy shoot, SF.B 11707, 10 mm. **g** *Sequoia abietina* (Brongniart) Erw. Knobloch, leafy shoot, S.P9101434, 10 mm. **h** *Taxodium dubium* (Sternberg) Heer, leafy shoot, SF.B 11431a, 10 mm. **i** *Taxodium dubium* (Sternberg) Heer, leafy shoot, SF.B 11470, 10 mm. **j** *Taxodium dubium* (Sternberg) Heer, leafy shoot, SF.B 11431b, 10 mm. **k** *Taxodium dubium* (Sternberg) Heer, leafy shoot, SF.B 11431c, 10 mm. **l** *Abies* sp., needles with enlarged bases, SF.B 11440, 10 mm. **m** *Pinus* sp., needles in double fascicle, SF.B 11430, 10 mm. **n** *Pseudotsuga kinkelini* (Mädlar) Kvaček, Teodoridis et Denk comb. nov., needle leaf, SF.B 11718, 10 mm. **o** *Pseudotsuga kinkelini* (Mädlar) Kvaček, Teodoridis et Denk comb. nov., needle leaf, SF.B 11419, 10 mm. **p** *Pseudotsuga kinkelini* (Mädlar) Kvaček, Teodoridis et Denk comb. nov., needle leaves, lectotype V.17169, 2 mm. **q** *Pseudotsuga kinkelini* (Mädlar) Kvaček, Teodoridis et Denk comb. nov., needle leaves, epitype SF.B 11420b, 2 mm. **r** *Torreya* aff. *nucifera* Siebold et Zuccarini, needle leaf, V 17176, 10 mm

Material: Eighteen leaves at Frankfurt/M., one in London, V.17168, three at Stockholm, S142884, S116317-01, S116317-02, S116314 (glass preparations).

Description: See Mädlar (1939, pp. 46–47).

Remarks: No additional information to that published by Mädlar (1939) has been obtained by the study of the newly collected material. The description corresponds to the previously published data in Mädlar (1939). For comments on the taxonomy, see Kvaček et al. (2008). The material from the new collection was used for a study of stomatal density as a proxy for atmospheric CO₂ concentration (Retallack 2001). Denk and Velitzelos (2002) noted that the abaxial epidermis of *Ginkgo* from Frankfurt shows only faint papillae, while in late Miocene material from northern Greece, the papillae were prominent and overarching the stomata.

Cupressaceae
Calocedrus Kurz

Calocedrus pliocaenica (Kinkelin) Kvaček, Teodoridis et Denk comb. nov.

Fig. 2d

1908 *Libocedrus pliocaenica* Kinkelin in Engelhardt and Kinkelin, p. 191, pl. 23, figs. 4, 5f (basionym)

1908 *Callitris brongniartii* sensu Kinkelin in Engelhardt and Kinkelin, p. 190, pl. 23, figs. 4, 5, pl. 23, fig. 5a–e

1908 *Algarites caulerpoides* Engelhardt and Kinkelin, p. 187, pl. 22, fig. 32

1939 *Libocedrus pliocaenica* Kinkelin; Mädlar, p. 42, pl. 4, figs. 1–6, text-figs. 12–14

1961 *Heyderia pliocaenica* (Kinkelin) Szafer, p. 28, pl. 7, figs. 9–12, pl. 8, figs. 1–7

Material: No syntype at SF (the originally selected lectotype by Mädlar 1939 was a seed figured in Engelhardt and Kinkel in 1908, pl. 23, fig. 4), only one slide with a twig available at Stockholm (S082691).

Neotype selected here: S082691 (fig. 2d)—foliage shoot (a duplicate from the material treated by Mädlar 1939).

Description of the neotype: Isolated foliage shoot, 15 mm long, up to 3.8 mm wide, shoot composed of six pseudowhorls with rounded to widely cuneate base and obtuse apices of two marginal and two facial leaves.

Remarks: Mädlar (1939) provided a detailed description of the original material destroyed during the war, which is sufficient for the identification of this rare conifer. Szafer (1961) included it into the genus *Heyderia* K. Koch, a younger synonym of *Calocedrus* Kurz.

Cryptomeria D. Don

Cryptomeria rhenana Kilpper

Fig. 15a–c

1953 *Cryptomeria* sp.; Sveshnikova 1953, p. 117, text-figs. 3.1, 3–4

1958 *Cryptomeria japonica* D. Don *fossilis* Sveshnikova; Kolakovskii, p. 322, pl. 3, fig. 1

1963 *Cryptomeria japonica* D. Don *fossilis* Sveshnikova, p. 225, pl. 12, figs. 9–10

1968 *Cryptomeria rhenana* Kilpper, p. 104, pl. 34, figs. 23–30, pl. 35, figs. 1–8, pl. 38, figs. 3–4

Material: Cuticle preparations S117681, 117682.

Description: Stomata rounded cyclocytic, subsidiary cells four to six, large, similar in form and size, stomatal complexes irregularly orientated.

Remarks: First, Sveshnikova (1953, 1963) described more complete twigs with this type of epidermal structure from the late Neogene sites of Georgia (Chokhati, Duab) and compared it with the living *Cryptomeria japonica* living in Japan and China. Complete fertile shoots from upper Miocene deposits of Rhineland including cuticle structure were investigated in detail by Kilpper (1968). Cuticle structure of the latter is the same as in the material of Frankfurt/M. (SF).

Glyptostrobus Endlicher

Glyptostrobus europaeus (Brongniart) Unger

Figs. 2e and 15j–l

1968 *Glyptostrobus europaeus* (Brongniart) Unger; Kilpper, p. 104, pl. 37, fig. 5

Material: Two fragmentary twigs V.17167 pro parte (assigned to *Callitris brongniartii* Saporta), cuticle preparations S 118207–118213.

Description: Twigs with helically disposed scale leaves, partly flat, not anatomically studied. Cuticle preparations showing macerated amphistomatic leaves, on abaxial cuticle ordinary cells with straight anticlines, 20–50 µm long and 7–20 µm wide, showing distinct crystal cavities, stomata cyclocytic, subsidiary cells in two to three circles, four to six cells per circle, the inner circle thick-walled, stomatal crypts irregularly orientated, two adjacent stomatal complexes usually sharing subsidiary cells.

Remarks: The twigs were identified as *Callitris brongniartii* Saporta obviously by Kinkel in. Two specimens correspond to sterile foliage recovered at the type locality of Alonissos (Iliodroma) Island (Mantzouka et al. 2019). The third may belong likely to *Sequoia abietina* (see below). The cuticles prepared by Florin in Stockholm correspond to the structure obtained from fertile twigs of *Glyptostrobus europaeus* from late Miocene deposits of Rhineland (Kilpper 1968, p. 104, pl. 37, fig. 5). It differs from that of *Taiwania* Hayata by stomata usually sharing subsidiary cells (Sveshnikova 1963, p. 212) and from *Sequoia* and *Sequoiadendron* by shorter ordinary cells in non-stomatal areas (Sveshnikova 1963, p. 212).

Several fossil species of *Glyptostrobus* were distinguished (e.g. Dorofeev 1974, Mai in Mai and Walther 1988) based on fossil seeds. These have not been recovered in the Pliocene deposits at Frankfurt/M.

Sequoia Endlicher

Sequoia abietina (Brongniart) Erw. Knobloch

Figs. 2f, g and 15i

1908 *Sequoia langsdorfii* (Brongniart) Heer sp. *plioaenica*-sensu Kinkel in Engelhardt and Kinkel in, p. 199, 278, pl. 24, figs. 1, 3–4

1908 *Taxodium distichum* Richard *plioaenicum* sensu Kinkel in Engelhardt and Kinkel in, p. 199, pro parte, pl. 23, fig. 21c

1908 *Pteris* sp. sensu Kinkel in Engelhardt and Kinkel in, p. 187, pl. 22, fig. 31

1908 *Rhamnus cathartica* Linnaeus *fossilis* sensu Engelhardt and Kinkel in, p. 264, pl. 32, fig. 32, fig. 30

1939 *Sequoia langsdorfii* (Brongniart) Heer sensu Mädlar, p. 37, pl. 1, figs. 38–39, pl. 3, figs. 8–9

Material: One fragmentary twig V.17167 pro parte (assigned to *Callitris brongniartii*), newly recovered material SF.B 11408 (?), 11410 (two shoots), 11411, 11415, 11432, 11461, 11472, 11474 (four shoots), 11475 (four shoots), 11476 (three shoots), S.P9101434 (one shoot), one shoot (S082692) and several cuticle preparations S118123–118130 from Stockholm.

Description: See Mädlar (1939, pp. 37–39).

Remarks: Leafy shoots embedded in glass preparations correspond in morphological features to those of modern *Sequoia sempervirens* (D. Don) Endlicher and fossil *S. abietina* type.

They were recorded from various plant assemblages of the European Neogene (e.g. Knobloch 1964; Kvaček 1976). The cuticle structure observed in the Stockholm specimens corresponds to fossils assigned to *Sequoia langsdorfii* (Brongniart) Heer by Kilpper (1968), pl. 38, figs. 5–7) from late Miocene deposits of Rhineland, and to other fossil records of the *Sequoia abietina* type in Europe.

Taxodium Richard

Taxodium dubium (Sternberg) Heer

Fig. 2h–k

1887 *Taxodium distichum* Richard *pliocenicum* Geyler et Kinkelin, p. 11, pl. 1, fig. 2

1908 *Taxodium distichum* Richard *pliocenicum* Geyler et Kinkelin; Engelhardt and Kinkelin, p. 198, 278, pl. 23, figs. 21a–b, d–h, fig. 30

1939 *Taxodium distichum* Richard *fossilis*; Mädlar, p. 39, pl. 4, fig. 7

Material: Only newly recovered material—leafy shoots—SF.B 11406 (three shoots), (?) 11407, 11409, 11412, 11413, 11424, 11425 (two shoots), 11426, (three shoots), 11427 (three shoots), 11428 (four shoots), 11429, 11430 (three shoots), 11431 (three shoots), 11437 (two shoots), 11441 (two shoots), 11442, 11443, 11444, 11445, 11446, 11447, 11448, 11449 (six shoots), 11450, 11451, 11452, 11453, 11454 (five shoots), 11455, 11456, 11457, 11458 (two shoots), 11459, 11460, 11462, 11463 (two shoots), 11464 (two shoots), 11465 (four shoots), 11466, 11467 (two shoots), 11468, 11469, 11470, 11471, 11472, 11474 (four shoots), 11475 (four shoots), 11476 (three shoots), one slide in Stockholm.

Description: See Mädlar (1939, pp. 39–41).

Remarks: Leafy shoots embedded in glass preparations correspond in morphological features to the type material from the Bohemian Miocene (see Kvaček 1976). Macerations of needles have not been successful, and the obtained preparations reveal only sub-macerated abaxial stomata orientated perpendicularly or obliquely to the needle length. Mädlar (1939) came to similar results when attempting cuticle macerations of his material. For a detailed discussion, see Kunzmann et al. (2009).

Pinaceae

Besides *Pinus*, also seed cones and seeds assigned to *Picea latissquamosa* (Ludwig) Geyler et Kinkelin, *Picea* sp., *Larix europaea* Lamarck et DC. *fossilis* Geyler et Kinkelin, *Keteleeria loehri* (Geyer et Kinkelin) Kinkelin and *Pseudolarix kaempferi* (Lambers) Gordon *fossilis* Florschütz were included in the Pliocene flora of Frankfurt/M. by Mädlar (1939). These records are not treated in the systematic part below. For the seed cones of *Pinus*, the revisions by Mai

(1986) and Kvaček et al. (2014a, b) and for *Keteleeria loehri* (Geyler et Kinkelin) Kinkelin, the revision by Kunzmann (2014) are accepted.

Abies Miller

Abies sp.

Fig. 2l

1908 *Abies* sp.; Engelhardt and Kinkelin, p. 220, pl. 27, figs. 4–5 (needles), p. 219, pl. 36, fig. 13 (seed)

1939 *Abies pectinata* DC. *fossilis* Mädlar, p. 19, pl. 1, figs. 10–17, pl. 3, figs. 6–7, text-figs. 5, 8, 10

Material: SF.B 11440 (one slide containing nine needles), a needle in Stockholm (S082695) of the material quoted by Mädlar (1939), one slide at V. 26362, otherwise missing.

Description: See Mädlar (1939, pp. 19–21).

Remarks: Material embedded in glass preparations does not allow studying anatomical structure, but the overall morphology, particularly the enlarged needle bases, is diagnostic of needles of fir. Detailed descriptions of needle anatomy by Mädlar (1939) also corroborate this generic assignment. According to Mädlar (1939, p. 21), these needle leaves differ from the Pliocene *Abies albuli* (Ludwig) Müller–Stoll from the locality Dernbach by morphology (rounded or emarginate tips).

Picea A. Dietrich

Picea omoricoides C.A. Weber

Fig. 15d–f

1898 *Picea omoricoides* C.A. Weber, p. 5, pls. 11–13

Material: One slide V. 17164 identified as *Picea*, cuticle preparations S117938–117942 coll. Stockholm.

Description: Macerated needles up to 2 mm wide, incomplete in length, rounded at apex, one side without stomata, ordinary cells coarsely undulate, ca. 15 µm wide, hypodermal cells straight-walled, similar in size, opposite side with longitudinally arranged narrow epidermal cells with deeply and regularly undulate anticlinal walls, stomata in five to eight rows, longitudinally aligned, bicyclic, subsidiary cells four to eight, with shallow undulate to pitted anticlinal walls, polar quadrangular, usually bordering two adjacent stomata, lateral subsidiary cells elongate, on one side usually shared among two adjacent stomata.

Remarks: The epidermal topography corresponds to that described for the Pliocene records of *Picea omoricoides* from Germany (Gerstungen and other sites, Mai and Walther 1988) and North Bohemia (Cheb Basin, Vildštejn Formation, Bůžek et al. 1985; Teodoridis et al. 2017).

Pinus Linnaeus

Pinus sp.

Fig. 2m

- 1908 Stiel von *Acer*, Engelhardt and Kinkel, p. 296, pl. 34, fig. 11b
 1939 Kurztriebe von *Pinus*; Mädler, p. 35, pl. 1, fig. 36

Material: SF.B 11433 and 11436 (two 2-needled fascicles), two missing specimens of 2- and 3-needled fascicles quoted by Mädler (1939).

Description: See Mädler (1939, p. 35).

Remarks: Needles in double fascicles have not been anatomically studied being enclosed in glycerol jelly between glass and plastic plates. They may belong to some of the associated seed cones but a straight-forward connection cannot be established.

Pseudotsuga Carrière

Pseudotsuga kinkelini (Mädler) Kvaček, Teodoridis et Denk comb. nov.

Figs. 2n–q and 15m–o

- 1939 *Podocarpus kinkelini* Mädler, p. 14, pl. 1, figs. 2–3, pl. 2, figs. 4–5, text-figs. 2, 6 (basionym)
 1988 *Cephalotaxus multiserialis* (Weyland) Mai et Walther, p. 71, pl. 6, fig. 23, text-fig. 7

Material: Two slides V.17169 and S082700; new material of isolated needles includes specimens SF.B 11418–11420a–c (one needle complete—epitype), 11421, 11422, 11423a, b and several cuticle preparations of SF.B 11419.

Lectotype suggested here: V. 17169 (fig. 2p).

Epitype suggested here: SF.B 11420b (fig. 2q).

Description: Leaves needle-like, up to 155 mm long, 3–4 mm wide, univeined, narrow cuneate at base, sessile, acute at apex, hypostomatic. Upper side consisting of thickly cutinised prosenchymatous epidermis composed of parallel aligned thick-walled cells. Lower side with a medial keel-like vein and two lateral zones bearing narrow papillate stomatal bands. Stomata monocyclic, longitudinally orientated, closely set in up to 13 rows, touching each other by lateral subsidiary cells, polar subsidiary cells partly shared by two adjacent stomata, rarely with additional cells, both bulging and thickly papillate. Ordinary cells outside the stomatal zones longitudinally aligned, similar to those of the adaxial epidermis.

Remarks: The stomatal topography as well as details of epidermal structure corresponds to the modern species of *Pseudotsuga* Carrière rather than to *Cathaya* Chun et Kuang. Mädler (1939) assigned these peculiar, long needles to *Podocarpus* L'Héritier ex. Persoon and mentioned great difficulties in investigating the epidermal parts. Also the presently studied material (SF.B 11419) was not easy for preparation of cuticles. The lower epidermis remained firmly attached to the leaf tissue in spite of strong maceration. *Cathaya* is fairly similar to the fossils discussed but lacks papillae within

stomatal bands and has quadrangular polar subsidiary cells (Kunzmann 2014). Delicate deciduous needle foliage of *Pseudolarix* Gordon may recall *Pseudotsuga kinkelini* but has stomatal zones smooth.

A long needle from the Pliocene of Auenheim corresponding also in the epidermal structure to the Frankfurt/M. specimens was misinterpreted as *Cathaya* (see Kvaček et al. 2008, p. 8, pl. 1, fig. 10, pl. 16, fig. 6, as *Cathaya* sp.). Szafer (1961), p. 26, pl. 7, figs. 1–6) referred needle fragments from the late Miocene of Poland with similar epidermal structure to *Podocarpus*. Foliage of *Pseudotsuga kinkelini* co-occurs with seed cones recently investigated by Kunzmann (2014) and assigned to *Pseudotsuga loehrri* (Geyler et Kinkel) L. Kunzmann.

By its acute leaf apex *Pseudotsuga kinkelini* is similar to the extant North American species. However, most modern species have shorter needles. *Pseudotsuga macrocarpa* (Vasey) Mayr from southern California is most similar by seed cone morphology to *P. loehrri* (Kunzmann 2014) as well as to *P. kinkelini* by needles up to 50 mm or even 60–80 mm long with acute tips. This modern species grows also in riparian habitats along with *Acer macrophyllum* Pursh and *Populus trichocarpa* Torrey et A. Gray (Barbour 1988).

Pseudotsuga sclereidea (Mädler) Kvaček, Teodoridis et Denk comb. nov.

Fig. 16a

- 1908 *Abies* sp.; Engelhardt and Kinkel, p. 221, pl. 27, figs. 7–8 11 (pro parte)
 1939 *Abies sclereidea* Mädler, p. 22, pl. 1, figs. 8–9, pl. 3, figs. 1–5, text-figs. 4, 11

Material: Two needle fragments of syntypes at Stockholm, no topotype material at SF.

Lectotype selected herein: S082707 (fig. 16a) coll. Mädler (1939).

Description: Needle fragments, the mesophyll tissue containing sclereids. For detailed description, see Mädler (1939), p. 22, pl. 1, figs. 8–9, pl. 3, figs. 1–5, text-figs. 4, 11).

Remarks: Although Mädler (1939) described in detail the epidermal structure of the needles, he included them within a new species of *Abies* being unaware that sclereids occur in needle tissue of several conifers. The stomatal topography clearly differs from *Abies* and indicates close affinity with *Pseudotsuga*. Fragmentary needles of the same kind were noted from the Pliocene of Auenheim and compared with the modern *P. menziesii* (Mirbel) Franco (Kvaček et al. 2008, p. 9, pl. 1, figs. 14–15, pl. 16, fig. 8).

Tsuga (Endlicher) Carrière

Tsuga (sect. *Tsuga*) sp.

1939 *Tsuga europaea* Menzel; Mädlar, p. 24, pl. 1, figs. 21–29

Material: No specimen at SF or NRM.

Remarks: Mädlar (1939) described 15 needles, all of which were destroyed in 1945. The figured needles correspond to some Pliocene records in Europe (Krościenko—Szafer 1947, partly as *T. caroliniana*, Berga—Mai and Walther 1988, as *Tsuga* sp., Auenheim—Kvaček et al. 2008, as *Tsuga* (sect. *Tsuga*) sp.). Most other records of *Tsuga* are based on seed cones including that of *T. europaea* Menzel (Kunzmann and Mai 2005).

Sciadopityaceae Luerssen

Sciadopitys Siebold et Zuccarini

Sciadopitys tertiaria Menzel

Fig. 15g, h

1908 *Abies* sp.; Engelhardt and Kinkel, p. 220, pl. 27, fig. 6

1922a *Sciadopitys tertiaria* Menzel; Florin, p. 3, pl. 1, figs. 1–4

1922b *Sciadopitys tertiaria* Menzel; Florin, p. 263, figs. 2c–e

1939 *Sciadopitys tertiaria* Menzel; Mädlar, p. 36

Material: Two slides, S118040, 118054.

Description: See Florin (1922a, b).

Remarks: The material at hand was recovered in collections of the previous working place of Rudolf Florin at Stockholm and represents originals to the paper mentioned above. According to Weyland et al. (1967), Pliocene and living differ from Miocene *Sciadopitys* in the lack of the papillate margin of the stomatal zone, which is distinctly papillate in the Miocene material. However, the studied samples from the Pliocene of Frankfurt do show narrow papillate rows along the stomatal zone, probably not noted by Florin. Hence, the argument to establish a Miocene species *S. marcodurensis* Weyland et al. is not valid.

Taxaceae Gray

Taxus Linnaeus

Taxus aff. *baccata* Linnaeus

Fig. 16b, c

Material: One slide, S082704.

Description: Needle fragments, 2–2.5 mm wide, incomplete in length, tip shortly pointed, leaves hypostomatic, adaxial cuticle smooth, anticlinal walls straight to slightly bent, outlines of unspecialised cells isodiametric to slightly elongate polygonal, in sub-parallel rows, 25–50 µm in diameter, abaxial cuticle thick, two longitudinal stomatal bands consisting of five stomatal rows, completely covered by papillae, stomata longitudinally orientated, amphicyclic, with strong Florin rings, widely disposed and not sharing subsidiary cells, guard cell pairs deeply sunken, surrounded by four to six subsidiary cells, medial and both lateral non-stomatal zones partly

smooth, partly papillate halfway towards stomatal bands, unspecialised cells straight-walled, quadrangular elongate, 40–120 µm long and 20–30 µm wide, anticlinal walls straight to slightly curved, smooth.

Remarks: The single microscopic slide available was identified as *Taxus francofurtana* Florin on the label with a note “orig. Florin, pl. 8, fig. 19, pl. 9, figs. 9–12”. Florin probably intended this material to be included in a more extensive revision on fossil *Cephalotaxus* and *Taxus* (see Seward and Edwards in Boulter and Kvaček 1989, p. 62), but this revision remained unpublished. According to its epidermal structure, the specimen differs from *T. inopinata* Givulescu (1973, 1975) from the Romanian Pannonian and from *Taxus* sp. 2 sensu Kvaček (1984) from the Pliocene of North Bohemia because the abaxial papillate zones along the stomatal bands are wider, reaching halfway to the stomatal bands. In the Romanian material, papillae are confined to the stomatal areas and also in the fragment from the Bohemian Pliocene/Pleistocene described as *Taxus* sp. 2 sensu Kvaček (1984), papillae densely covering the stomatal bands are almost lacking on adjacent non-stomatal zones (Kvaček 1984, fig. 4a, e). The Pliocene record of *Taxus* from Willershausen, identified as *Taxus baccata* L. *fossilis* (Straus 1952, p. 20, pl. 4, figs. 6–7, pl. 7, figs. 28, 30) does not differ from that of Frankfurt according to the epidermal anatomy and may belong to the same fossil species. We follow Macovei (2013), who recommended not using independent fossil species names for remains that represent close ancestors of *Taxus baccata* L. The Oligocene *T. engelhardtii* Kvaček differs by the fully papillate abaxial medial area (Kvaček 1976, 1984).

Cephalotaxus Siebold et Zuccarini

Cephalotaxus pliocaenica Mädlar

1939 *Cephalotaxus pliocaenica* Mädlar, p. 18, pl. 1, figs. 6–7, pl. 2, figs. 6–9, text-figs. 3, 3, 7, 9

Material: The type material is destroyed and no new topotype material is available at SF.

Remarks: Although no material of this conifer described by Mädlar (1939) has been recovered in the collections available, the description and illustrations are sufficient for the recognition of this fossil species in the Pliocene flora of Frankfurt/M. Similar needles were recorded in the Romanian Pannonian and assigned to *Cephalotaxus pliocaenica* by Givulescu (in Givulescu and Olos 1973, p. 32, pl. 12, figs. 4–6, pl. 14, pl. 1, pl. 15, figs. 7–8). A single fragment from the early Miocene Cypris formation of north Bohemia (Kvaček 1984) shows sclereids in the leaf tissue not noticed in the type material of *Cephalotaxus pliocaenica* Mädlar, although it matches the illustrations and descriptions of Mädlar (1939) in several other anatomical features. It is also distinguished by the rounded leaf base. Another European Miocene record

◀ **Fig. 3** **a** *Magnolia liblarensis* (Kräusel et Weyland) Kvaček, leaf fragment, SF.B 12438, 10 mm. **b** *Magnolia waltheri* Kvaček, Teodoridis et Denk sp. nov., incomplete leaf, SF.B 12169, 10 mm. **c** *Sassafras* cf. *ferretianum* Massalongo et Scarabelli, complete leaf, SF.B 12151, 10 mm. **d** *Smilax* sp., incomplete leaf with entire margin (stars), SF.B 11529, 10 mm. **e** Gramineae gen. et sp. indet., leaf fragment, V 26395, 10 mm. **f** *Buxus pliocaenica* Saporta, complete leaf, SF.B 12285, 10 mm. **g** *Buxus pliocaenica* Saporta, shortly petiolete leaf, S082706, 10 mm. **h** *Buxus pliocaenica* Saporta, leafy shoot, S082706, 10 mm. **i** *Pachysandra europaea* Kvaček, Teodoridis et Denk sp. nov., incomplete leaf, holotype SF.B 12393, 10 mm. **j** *Liquidambar europaea* A. Braun, incomplete pentalobate leaf, SF.B 12158, 10 mm. **k** *Parrotia pristina* (Ettingshausen) Stur, incomplete leaf, SF.B 12161, 10 mm. **l** *Cercidiphyllum crenatum* (Unger) R.W. Brown, leaf fragment, SF.B 12466, 10 mm

of *Cephalotaxus* sp. (according to Kvaček 1976, i.e. *Taxus grandis* (Steger) Kräusel partim) is too incompletely preserved to be assigned to a fossil species. The Oligocene species *C. parvifolia* (Walther) Kvaček et Walther differs in smaller needles and indistinctly limited stomata within the stomatal bands (Walther and Kvaček 2007). Comparable fossil species of *Cephalotaxus* are known also from the Oligocene of China (Shi et al. 2010) and the Miocene of western North America (Kvaček and Rember 2000).

Torreya Arnott

Torreya aff. *nucifera* Siebold et Zuccarini

Fig. 2r

1908 *Torreya nucifera* Siebold et Zuccarini *fossilis* Kinkelin in Engelhardt and Kinkelin, p. 191, pl. 23, figs. 6–8 pro parte (foliage)

1939 *Torreya nucifera* Siebold et Zuccarini *fossilis* Kinkelin; Mädlar, p. 13, pl. 2, figs. 1–3

Material: All original material listed by Engelhardt and Kinkelin (1908) and Mädlar (1939) was destroyed except two needle and epidermis preparations kept at NRM (S082693, S082791). Another specimen was found at the BMNH, V. 17176. No new material is available at SF.

Description: See Mädlar (1939, pp. 13–14).

Remarks: The fossil leaf material corresponds in most respects to extant *T. nucifera* distributed in Japan. A more detailed comparative study of foliage between living and fossil representatives of *Torreya* is needed to establish their relationships. It is probable that dispersed needles and seeds in the Pliocene of Frankfurt/M. represent a single biological species according to the whole plant concept of Kvaček (2008). In any case, the foliage deserves an independent fossil species name, as done for the seeds (*T. schulzii* Gregor, van der Burgh, Peters, Pinggen—Gregor et al. 2000).

Angiospermae

Magnoliaceae Jussieu

Magnolia Linnaeus subgen. *Magnolia*

Magnolia liblarensis (Kräusel et Weyland) Kvaček

Figs. 3a and 16j–l

1939 Laubblatt sp.; Mädlar, p. 144, pl. 10, fig. 26, pl. 13, figs. 7–9

1959 *Papilionaceophyllum liblarensense* Kräusel et Weyland, p. 111, pl. 24, figs. 37–41, pl. 25, figs. 42–47, pl. 26, fig. 48, text-figs. 10–11

1979 *Magnolia liblarensis* (Kräusel et Weyland) Kvaček, p. 172, pl. 37, figs. 2–5

Material: SF.B 12438 and cuticle slides B 12438.1, 2.

Description: Fragment of an entire-margined leaf, apex missing, probably acute, lamina > 20 mm wide, venation brochidodromous, primary vein thick, straight, secondary veins much thinner, widely spaced, looping well within margin, one to four intersecondary veins, tertiary veins sinuous, higher-order veins reticulate. Lamina in transmitted light finely punctate due to secretory cells. Adaxial cuticle smooth, unspecialised cells polygonal, 15–25 µm in diameter, with anticlinal walls narrowly undulating and curved, abaxial cuticle smooth, unspecialised cells polygonal, with Ω-shaped anticlines, paracytic stomatal complexes rounded, 25 µm in diameter, guard cell pairs faintly visible within pairs of subsidiary cells, pore linear to very narrow and short, ledges thin, solitary simple rounded trichome bases rarely observed, lense-shaped rounded oil cells in mesophyll tissue of different sizes and frequent.

Remarks: The previously published material identified as “Laubblatt sp. E” by Mädlar (1939), p. 144, pl. 10, fig. 26, pl. 13, figs. 7–9) shows the same cuticle pattern and may expand the above characteristics of this record (see detailed morphological description by Mädlar 1939 and the reconstructed leaf form of several fragments). Contrary to the type of *Magnolia liblarensis* from the Rhineland Miocene (Kräusel and Weyland 1959, as *Papilionaceophyllum liblarensense*) and most other Miocene occurrences in Europe (see Kovar-Eder and Hably 2006; Schneider 2004, as *Falciculis varians* Schneider), the fragment recovered here as well as the illustrations by Mädlar (1939) from the same site differs in glabrous laminas. Thus, the fossil species *M. liblarensis* may turn out to be heterogeneous or is highly variable in pubescence, as documented by Fischer and Butzmann (2000).

Several living Magnoliaceae with similar epidermal patterns (undulate anticlinal walls, rare or lacking pubescence) have been noticed in the modern cuticle collection of Z. Kvaček: *Magnolia gustavii* King (Assam), *M. henryi* Dunn (Laos), *M. nitida* W.W. Smith (Yunnan), *M. championii* Benthham (Guangxi), *M. pterocarpa* Roxburgh (Chittagong), *M. liliifera* (Linnaeus) Baillon (Central Vietnam) and *M. elegans* (Blume) H. Keng (Java).

Magnolia subgen. *Yulania* (Spach) Reichenbach
Magnolia waltheri Kvaček, Teodoridis et Denk sp. nov.
 Figs. 3b and 16f–i

Material: SF.B 12153, 12155, 12156, 12169, cuticle slides SF.B 12155.1–4, B 12169.1, 2.

Holotype established here: Specimen SF.B 12155 (fig. 3b), cuticle slides SF.B 12155.1–4.

Derivatio nominis: Remembering late Prof. Harald Walther, expert in fossil leaf morphology and anatomy.

Description: Leaves long petiolate, petiole > 15 mm long, lamina ovate, 80 mm long, > 40 mm wide, entire-margined, apex bluntly acute, base widely cuneate, venation camptodromous, primary vein stout at base, much thinner apically, secondary veins irregularly spaced, more closely spaced at base than towards apex, bent, forked and looping at margin, intersecondaries rare and single, intercostal tertiary veins straight, perpendicular to secondary veins. Adaxial cuticle smooth, hairless, polygonal cells with straight anticlines without thickenings 20–30 µm in diameter, abaxial cuticle very thin, ordinary cells domed, stomata not sunken, brachyparacytic, guard cell pairs broadly elliptic to transversally elliptic, 15 µm long, stomatal ledges slightly thickened in the middle, forming spindle-shaped narrow outer aperture. Mesophyll tissue filled with lens-shaped oil cells 25–50 µm in diameter.

Remarks: Thin cuticles, mesophyll oil cells and the preserved epidermal structure refer these leaf fragments to the Magnoliales. The overall venation and the morphology compare well with foliage of deciduous magnolias. The fragment of *M. liblarensis* described above clearly differs in epidermal patterns, namely the undulate anticlines, non-papillate surface and distinct roundish stomatal complexes. *Magnolia waltheri* resembles by its stomata patterns *Laurophyllum kinkelinii* Kvaček (2004) from the Oligocene flora of Flörsheim. Walther (2003), p. 137, text-fig. 3) refers a similar leaf impression from the early Oligocene of Saxony to *Magnolia* sp. Similarly, so far described Neogene species based on foliage are usually not characterised anatomically (e.g. *M. diana* Unger, *M. fraterna* Saporta, *M. mirabilis* Kolakovskij), and thus, their affinity to Magnoliales cannot be established with certainty.

Magnolia waltheri matches best in epidermal anatomy (thin cuticles, straight-walled anticlines) and morphology (widely cuneate leaf base, tertiary venation) modern deciduous magnolias, such as *Magnolia kobus* DC. (Japan). *Magnolia salicifolia* (Siebold et Zuccarini) Maximowicz (Japan) resembles the fossil species also by its doomed abaxial cells. *Magnolia waltheri* probably represents foliage belonging to seeds assigned to *M. cor* Ludwig and described from the Pliocene flora of Frankfurt/M. by Mädler (1939). According to Mai (1975, p. 564), the seeds are comparable with the extant *M. kobus*.

Lauraceae Jussieu
Sassafras J. Presl
Sassafras cf. *ferretianum* Massalongo et Scarabelli
 Figs. 3c and 16d, e

Material: SF.B 12151, 12157, cuticle preparations SF.B 12157.1–3.

Description: Leaves petiolate, petiole up to 19 mm long, lamina ovate, 80 mm long, 23–40 mm wide, entire-margined, apex bluntly acute, base widely cuneate, venation camptodromous, primary vein stout at base, much thinner apically, secondary veins irregularly spaced, more closely spaced at base than towards apex, bent, forked and looping at margin, intersecondaries rare and single, intercostal tertiary veins straight, forming acute angles with secondary veins. Adaxial cuticle smooth, hairless, reflecting polygonal cells with straight anticlines without thickenings 20–30 µm in diameter, abaxial cuticle very thin, ordinary cells doomed, stomata not sunken, brachyparacytic, guard cell pairs broadly elliptic to transversally elliptic, 15 µm long, stomatal ledges slightly thickened in the middle, forming spindle-shaped narrow outer aperture. Mesophyll tissue filled with lens-shaped oil cells 25–40 µm in diameter.

Remarks: Similar thinly cutinised leaf compressions with oil cells may belong to the Lauraceae, most probably to deciduous plants. The preserved compressions show similar morphological features as the leaf fragment assigned to the same taxon from the Pliocene of Auenheim (Kvaček et al. 2008).

Smilacaceae Ventenat
Smilax Linnaeus
Smilax sp.
 Fig. 3d

Material: SF.B 11528, 11529.

Description: Leaves incomplete, petiolate, lamina broadly ovate, base shallowly cordate-concavo-convex, apex missing, margin entire, venation campylodromous, primary veins 5, secondary veins very thin forming wide meshes with higher-order vein matrix ascending towards the margin and looping far from it.

Remarks: The few foliage remains at hand surely belong to the Smilacaceae because of the characteristic gross morphology and venation. Both specimens fall within the morphological variation of *Smilax sagittifera* Heer sensu Hantke (1954) and *S. weberi* Wessel. Similar leaf shapes are found in a great number of modern species (Denk et al. 2015).

Gramineae Jussieu
 Gramineae gen. et sp. indet.
 Fig. 3e

Material: V.26392, 26393, 26394, 26395.

Description: Narrowed strip-like leaf fragments, entire-margined and parallel veined.

Remarks: Grass-like foliage fragments not identifiable to a genus noted also by Mädlér (1939, p. 49).

Buxaceae Dumortier

Buxus Linnaeus

Buxus pliocaenica Saporta

Figs. 3f–h and 16m, n

1876 *Buxus pliocaenica* Saporta in Saporta and Marion, p. 144, pl. 32, figs. 6–8

1908 *Buxus sempervirens* Linnaeus *fossilis* Engelhardt in Engelhardt and Kinkelin, p. 260, pl. 33, figs. 1a–r, 2

1939 *Buxus sempervirens* Linnaeus *fossilis* Engelhardt; Mädlér, p. 109, pl. 13, figs. 1–2

Material: Original slides of Mädlér (1939) at Stockholm, S082705, S082706, and at BMNH, V.17174, numerous leaf compressions in glass preparations at SF.

Description: Cuticles of both leaf sides thick, adaxial cuticle reflecting thick-walled unspecialised cells with straight anticlines, only slightly variable in diameter, abaxial cuticle smooth, unspecialised cells similar to those of the abaxial cuticle, stomata anomocytic, broadly elliptic, with I-pieces at poles, ledges thick, forming broadly elliptic pore extending nearly to the poles.

Remarks: Mädlér (1939) described for the first time the cuticle structure of this foliage. Subsequent authors (Kvaček et al. 1982, Hably and Kvaček 1997, Kvaček et al. 2008, p. 29) partly revised Mädlér's interpretation and recognised the independent status of the fossil species following the original concept of Saporta (in Saporta and Marion 1876) who excluded this fossil species from the modern *Buxus sempervirens* Linnaeus.

Pachysandra A. Michaux

Pachysandra europaea Kvaček, Teodoridis et Denk sp. nov.

Figs. 3i, 16o and 17a

Material: A single leaf compression and cuticle preparations.

Holotype: SF.B 12393 (fig. 3i), cuticle preparations SF.B 12393.1–2.

Derivatio nominis: Referring to the typical occurrence of the species.

Description: Leaf ovate, 36 mm long, 18 mm wide, coriaceous and thickly cutinised, widely and shallowly bluntly serrate, base decurrent, teeth 3 on each leaf side, their size diminishing towards leaf base, venation pinnate, festooned semicraspedodromous. Adaxial cuticle thick, ordinary cells 38 µm in diameter, polygonal, anticlinal cell walls smooth, straight to little curved, abaxial cuticle thick, ordinary cells the same as in adaxial cuticle, stomata broadly elliptic, 50 × 40 µm in size, irregularly orientated, anomocytic (to

cyclocytic), with a thick stomatal ring inside, I-pieces at poles, aperture between guard cells linear, short massively cutinised trichomes simple, subulate, 50–80 µm long and 30 µm thick, on margin. Oil cells in the mesophyll tissue disc-shaped, 30–50 µm in diameter.

Remarks: The epidermal structure including the stomata corresponds to the modern representatives of *Pachysandra* (see also Baranova 1980). Fossils of *Pachysandra* have been reported from the European Palaeogene as rare seeds (e.g. Mai and Walther 1985, as *P. ascidiiformis* Mai) and pollen (Krutzsch 1966; also noted in the Eocene of Axel Heiberg Island, McIntyre 1991). To our knowledge, fossil foliage of *Pachysandra* has not previously been known. Straus (1992, p. 58) mentioned a record of *Pachysandra* for the Pliocene Willershausen flora without further description or documentation.

Both morphological and leaf anatomical traits of the single compression available indicate its affinity with this evergreen to semi-evergreen subshrub distributed by two or three extant species (*P. terminalis* Siebold et Zuccarini, *P. axillaris* Franchet and *P. stylosa* Dunn) in East Asia and by one species (*P. procumbens* A. Michaux) in southeastern USA. The fossil at hand is best comparable by its glabrous lamina and the leaf form with *P. terminalis* distributed in Japan and China (Gansu, Hubei, Shaanxi, Sichuan, Zhejiang) in shady and damp land in forests at altitudes between 1000 and 2600 m a.s.l. (Wu and Raven 2008, p. 331). Two other extant species from East Asia; *P. axillaris* and *P. stylosa* differ by the rounded to cordate leaf base and thick pubescence, *P. procumbens* from the USA by the coarsely toothed margin and hairy leaves, both adaxially and abaxially.

Altingiaceae Lindley

Liquidambar Linnaeus

Liquidambar europaea A. Braun

Fig. 3j

1836 *Liquidambar europaea* A. Braun in Buckland, p. 513

Material: SF.B 12158.

Description: Leaf incomplete, pentalobate, lobes with glanular crenulate margin.

Remarks: The single specimen of *Liquidambar europaea* in the Pliocene of Frankfurt/M. confirms the rarity of this element in this flora. It is also known from the carpological record of Frankfurt (Supplementary material File 1). *Liquidambar* is lacking in the Pliocene of Auenheim (Kvaček et al. 2008) and Willershausen (Knobloch 1998). The pentalobate leaf form of this fossil species is more common than the trilobate one in the late Neogene of Europe (see Knobloch and Kvaček 1976; Hummel 1983). Zhilin (1974) noted that according to Smith (1967) *Liquidambar styraciflua* produces two leaf forms on every branch differing in the depth of the lobes and the length of the petioles. This variation does not concern the number of lobes, though. According to Hummel (1983), epidermal characteristics

of a pentalobate leaf fragment from the Pliocene of southern Poland indicate a closer relationship of Pliocene records of *Liquidambar europaea* to the modern *L. orientalis* Miller.

Hamamelidaceae R. Brown
Parrotia C.A. Meyer

◀ **Fig. 4** **a** *Gleditsia pliocaenica* Kvaček, Teodoridis et Denk sp. nov., incomplete leaflet, paratype SF.B 12413, 10 mm. **b** *Gleditsia pliocaenica* Kvaček, Teodoridis et Denk sp. nov., incomplete leaf, holotype SF.B 12414, 10 mm. **c** aff. *Podocarpium* sp., complete leaflet, SF.B 12432, 10 mm. **d** *Crataegus pentagynoides* Kvaček, Teodoridis et Denk sp. nov., simple leaf with long petiole, SF.B 12145, 10 mm. **e** *Crataegus pentagynoides* Kvaček, Teodoridis et Denk sp. nov., pinnately deeply dissected leaf, V26395, 10 mm. **f** *Crataegus pentagynoides* Kvaček, Teodoridis et Denk sp. nov., pinnately deeply dissected leaf, SF.B 12152, 10 mm. **g** *Crataegus pentagynoides* Kvaček, Teodoridis et Denk sp. nov., pinnately deeply dissected leaf, SF.B 12170, 10 mm. **h** *Malus* sp., complete leaf with serrulate margin, SF.B 12165, 10 mm. **i** ? *Prunus* sp., incomplete leaf, SF.B 12387, 10 mm. **j** *Rosa* sp., complete leaflet, SF.B 12172, 10 mm. **k** *Rosa* sp., complete leaflet, SF.B 12171, 10 mm. **l** *Sorbus* sp., leaflet, SF.B 12167, 10 mm. **m** *Spiraea* sp., obovate leaf, SF.B 12168, 10 mm

Parrotia pristina (Ettingshausen) Stur

Fig. 3k

1851 *Styrax pristinum* Ettingshausen, p. 19, pl. 3, fig. 9

1867 *Parrotia pristina* (Ettingshausen) Stur, p. 192, pl. 5, figs. 2–3

Material: SF.B 12159, 12161.

Description: Incomplete leaves, 60 and 55 mm long, 35 and 45 mm wide, base cuneate to cordate, apex not preserved, margin entire to undulate, venation camptodromous, midrib strong, moderate, secondaries straight, opposite (basal pair) to alternate and looping, tertiary veins perpendicular, straight, venation of higher-order reticulate, veinlets simple branched.

Remarks: A few compression fossils show the characteristic basal venation and asymmetry found in Hamamelidaceae and this fossil species. The material at hand is not complete enough to resolve the exact systematic position of this fossil taxon (see previous discussions in Bůžek 1971; Kvaček et al. 2011). A closely related modern species is *Parrotia persica* (DC.) C.A. Meyer.

Cercidiphyllaceae Engler

Cercidiphyllum Siebold et Zuccarini

Cercidiphyllum crenatum (Unger) R.W. Brown

Fig. 3l

1850 *Dombeyopsis crenata* Unger, p. 448

1859 *Grewia crenata* (Unger) Heer, p. 42, pl. 109, figs. 12–21, pl. 110, figs. 1–11

1935 *Cercidiphyllum crenatum* (Unger) R.W. Brown, p. 575, pl. 68, figs. 2, 6, 8–10

Material: SF.B 12466.

Description: Leaf fragment, probably ovate, petiolate, 36 mm long, 14 mm wide, base rounded, apex not preserved, margin slightly crenulated, venation palmate, primary veins 5, straight (midrib) to curved (lateral veins), secondary and tertiary veins ramified, areolation poorly developed.

Remarks: A single fragmented leaf compression belongs to this common deciduous element of the northern hemispheric Cenozoic flora based on its morphology (venation palmate, 5-veined, margin regularly closely uniformly crenate).

Fossil populations slightly differ in fruit morphology as shown in foliage shoots with attached fruits (Smiley and Rember 1985; Kvaček and Konzalová 1996). It is closely similar to the modern species *C. japonicum* Siebold et Zuccarini from Japan and China, a deciduous tree inhabiting riparian forests.

Fabaceae Lindley (Leguminosae Jussieu)

Gleditsia Linnaeus

Gleditsia pliocaenica Kvaček, Teodoridis et Denk sp. nov.

Figs. 4a, b and 17b

Holotype: Leaflet compression on glass slide SF.B 12414 (fig. 4b) and cuticle preparation SF.B 12414.1 (fig. 17b).

Paratypes: Leaflets SF.B 12412–12413, 12415–12422.

Derivatio nominis: Referring to the geological age of the Klärbeckenflora, Frankfurt/M.

Description: Leaflets detached, sessile or exceptionally with very short petiolule, 22–40 mm long, 12–33 mm wide, narrowly to broadly ovate, base asymmetrical, rounded to cuneate, apex broadly acute, margin irregularly, simple bluntly serrate except entire-margined base, teeth simple, shallow asymmetrically rounded, venation semi-craspedodromous, craspedodromous, primary vein straight or slightly curved, secondary veins in up to seven pairs with single intersecondaries, looping widely along the margin, lateral veinlets entering the margin into teeth, tertiary veins forming asymmetrical meshes with higher-order vein matrix. Epidermal structure of the holotype: adaxial cuticle smooth, ordinary cells polygonal, 25–40 µm in diameter, anticlinal walls slightly bent, simple thin trichomes up to 150 µm dispersed on veinlets, abaxial cuticle smooth, ordinary cells with curved or bent anticlinal walls, mostly 30 µm in diameter, over veins quadrangular, 12–15 µm wide, 25–75 µm long, solitary elliptical thin-walled tri-chome bases 25 × 15 µm in size, stomata irregularly disposed, elliptic, irregularly sized, average 25 µm long, 15 µm wide, ? anomocytic, stomatal ledges slightly thickened, aperture boat-shaped, slit linear.

Remarks: Similar leaflets were described as *Gleditsia* by Guo and Zhou (1992) from the Miocene of China and by Kvaček et al. (2011) from the Miocene of southwestern Europe (Arjuzanx). *Gleditsia suevica* Rüffle (1963) and the foliage described as *Podogonium oehningense* (Koenig) Kirchheimer sensu Rüffle (1963) of the Miocene of Germany show a similar structure of the adaxial as well as abaxial epidermis and pubescence but differ by the entire margin and petiolulate leaflets. The modern *Gleditsia caspica* Desfontaines produces similar foliage and might be the closest

extant relative of the fossil taxon; it is a typical element of the lowland Hyrcanian forests associated with other relic elements, such as *Pterocarya*, *Albizzia* and *Parrotia* (Denk 1998). *Gleditsia pliocaenica* differs from *G. caspica* in broader asymmetrically ovate leaflets and a distinctly crenulate lamina.

aff. *Podocarpium* A. Braun

aff. *Podocarpium* sp.

Fig. 4c

Material: SF.B 12432.

Description: Leaflet, sessile, narrow ovate, 25 mm long, 9 mm wide, rounded at base and apex, margin almost entire, venation brochidodromous, primary vein slightly bent, secondary veins steep, in six pairs, with rare single intersecondaries, tertiary veins reticulate.

Remarks: The single specimen is similar to *Gleditsia pliocaenica* based on its venation but might belong to a different genus of the legumes. Leaflets of *Podocarpium podocarpum* (A. Braun) Herendeen widely distributed in the European Neogene differ in fully entire margins and one stronger basal, asymmetrically disposed, secondary vein (Bůžek 1971, p. 98).

Rosaceae Jussieu

Crataegus Linnaeus

Crataegus pentagynoides Kvaček, Teodoridis et Denk sp. nov.

Fig. 4d–g

? 1855 *Crataegus oxyacanthoides* Göppert, (non Thuill.), pp. 38–39, pl. 26, fig. 1, nom. illegit

? 1930 *Crataegus oxyacantha* Linnaeus; Straus, p. 31, pl. 37, fig. 8, pl. 41, figs. 10–11

1992 *Crataegus* cf. *oxyacantha* Linnaeus fossilis (= *C. laevigata*); Straus, p. 52

1998 *Crataegus* aff. *oxyacanthoides* Göppert; Knobloch, p. 67, pl. 39, figs. 6–7

Holotype established here: SF.B 12170 (Fig. 4g).

Paratypes: SF.B 12152, 12154, 12166.

Derivatio nominis: Expressing similarity to the foliage to the modern *Crataegus pentagyna* Waldstein.

Description: Leaves simple, long petiolate, petiole up to 30 mm long, lamina up to 35 mm long, 20–35 mm wide, pinnately deeply dissected into 1–2 pairs of simple, widely serrate lobes departing from main axis at 90° or at very wide angles.

Remarks: Such leaves are rarely found in the European Pliocene and have usually been ascribed to *Crataegus* (e.g. from the Hungarian site Pula, Hably and Kvaček 1997; and from the German Pliocene of Willershausen, Knobloch 1998) but a closer assessment of the relationship has been rarely

attempted. Indeed, the foliage alone may hardly afford a firm basis to determine the systematic position of a fossil species of *Crataegus* without details of pubescence, position of the leaf within the crown and without any other organs of the mother plant. Similar deeply dissected leaves are found in sect. *Pentagyna* in modern *C. pentagyna* (syn. *C. melanocarpa* Bieberstein) native to eastern South Europe, the Caucasus and Iran. Similar leaf forms are produced also in sect. *Crataegus*, e.g. *C. sakranensis* Hadač et Chrtek, *C. longipes* Pojarkova ex Christensen (see Christensen 1992).

Malus Miller

Malus sp.

Fig. 4h

Material: SF.B 12165.

Description: Leaf petiolate, petiole 13 mm long, lamina ovate, 78 mm long, apex acuminate, base obtuse to widely cuneate, margin simple serrulate, venation eucamptodromous to brochidodromous, secondary veins irregularly spaced, strongly bent, small veins departing from secondary veins and entering teeth.

Remarks: This single compression matches in leaf morphology, particularly the acuminate apex, leaves of the modern *Malus baccata* (Linnaeus) Borkhausen (“Siberian crab apple”) from northern Asia. The European *M. sylvestris* Miller differs in the short acute apex. Knobloch (1998) stated that his fossil species *Dicotylophyllum kvacekii* Erw. Knobloch (1998, p. 84, pl. 62, fig. 3) from the Pliocene of Willershausen showed a leaf gross morphology similar to *Euonymus* Linnaeus due to the characteristic venation, but also to *Malus*. Fossils of *Malus* are extremely rare, e.g. a carpological record from the Pliocene–Pleistocene of Italy (Martinetto et al. 2007).

Prunus Linnaeus

? *Prunus* sp.

Figs. 4i and 17c–e

2008 *Dicotylophyllum* cf. *heerii* Kvaček et Walther; Kvaček et al., p. 39, pl. 13, figs. 9–13, pl. 23, figs. 1–2

Material: SF.B 12387, cuticle preparations SF.B 12387.1–3.

Description: Leaf base cuneate, lamina 38 mm long, short petiolate, petiole fragmentary, lamina crenulate, primary vein firm, secondary veins simple or forking, intersecondaries present, secondary venation brochidodromous, small veins entering crenations, tertiary veins oblique to secondary veins, secondary veins to higher-order veinlets prominent, adaxial cuticle medium thick, smooth, outlines of unspecialised cells polygonal, anticlinal walls fine shallow undulate, trichome bases thickly cutinised, simple, rounded, star-like and surrounded by a simple ring of five subsidiary cells that are staining darker

than ordinary cells, mainly present on veins, abaxial cuticle slightly granular, smooth over veins, unspecialised cells polygonal, with strongly undulate anticlines, stomata cyclocytic, rarely anisocytic, guard cell pairs broadly elliptic, to circular, 25–37 µm long and 20–25 µm wide, periphery and ledges punctate, pore broadly elliptic, 12 µm long, 10 µm wide, 1-pieces thin., subsidiary cells 5–6 arranged in a simple ring, slightly darker than unspecialised cells.

Remarks: Similar leaf compressions were referred to as *Dicotylophyllum* cf. *heerii* (Engelhardt) Kvaček et Walther in the Pliocene of Auenheim (Kvaček et al. 2008, p. 39, pl. 13, figs. 9–13, pl. 23, figs. 1–2) and compared to *Prunus laurocerasus* Linnaeus. The Miocene flora of Arjuzanx included also leaf compressions having similar leaf morphology and epidermal anatomy (as “*Viburnum*” *atlanticum* Ettingshausen, Kvaček et al. 2011, pro parte, pl. 8, fig. 24). A possible modern analogue is *Prunus laurocerasus* Linnaeus from southeastern Europe to northern Iran or *P. lusitanica* Linnaeus from southern Europe, Madeira to the Canary Islands. The epidermal structure, namely cyclocytic, rarely anisocytic stomata and trichome bases on both leaf sides, makes the comparison with *Prunus laurocerasus* with hairless leaves equivocal. Similar epidermal structure is found in some Theaceae. *Prunus lusitanica* differs in incompletely amphicyclocytic stomata (Rasche and Kovar-Eder 2009). The so far described fossil records compared with *Prunus laurocerasus* Linnaeus are from upper Oligocene deposits of Kazakhstan (see Zhilin 1974, as *Laurocerasus praeofficinalis* Zhilin) to Pliocene deposits of southern Europe (as *Laurocerasus officinalis* Roemer *pliocenica* Laurent see Marty in Laurent 1904 or *Laurocerasus officinalis* Roemer fossilis see Palamarev et al. 2005), but none of them was confirmed by the leaf epidermal structure.

Rosa Linnaeus

Rosa sp.

Fig. 4j, k

Material: SF.B 12171, 12172, 12173, 12174, 12175.

Description: Leaflets with sharply simple serrate margin and dense semicraspedodromous rosoid venation.

Remarks: Similar foliage was described from various European Miocene floras, e.g. Kreuzau (Ferguson 1971, as Taxon No. XXXI. *Rosa*). The available remains consisting of isolated and mostly fragmentary leaflets are difficult to compare to particular modern or fossil species.

Sorbus Linnaeus

Sorbus sp.

Fig. 4l

Material: SF.B 12167.

Description: A single detached leaflet, sessile, oblong, base asymmetrical, apex bluntly acute, coarsely simple serrate to

entire-margined, venation craspedodromous and eucapto-dromous (when entire-margined), primary vein straight, secondary veins regularly spaced, bent, occasionally forking, secondary veins in up to 15–18 pairs, marginal teeth simple apiculate.

Remarks: The leaflet belongs to a compound leaf because of its sessile asymmetrical base. Venation and serration patterns place this single specimen into *Sorbus* sect. *Sorbus*. Epidermal details were not observed. The modern species *S. aucuparia* Linnaeus (Europe) and *S. americana* Marshall are closely similar. Of several fossil species, none matches exactly in morphological details (e.g. *Sorbus lanceolata* Tanai et Suzuki 1965 from the Neogene of Japan with widely disposed teeth on leaflets, *Sorbus* cf. *uzenensis* Huzioka sensu Erw. Knobloch 1998 with dense marginal serration).

Spiraea Linnaeus

Spiraea sp.

Fig. 4m

Material: SF.B 12168.

Description: Leaf obovate, shortly petiolate, petiole stout, 3 mm long, lamina 30 mm long, 15 mm wide, finely serrate in the upper half, below entire-margined, venation eucamptodromous and craspedodromous, primary vein straight, secondary veins in eight pairs, in the lower part steep, higher up at moderate angles, with densely spaced lateral veinlets entering the teeth, tertiary veins oblique to the secondary veins.

Remarks: This is the only leaf compression referable by its morphology to *Spiraea*. Of the living representatives, mostly deciduous shrubs distribute in temperate Eurasia and North America. Several extant species are fairly similar to the fossil, e.g. *S. trichocarpa* Nakai of Korea and *S. douglasii* Hooker (incl. subsp. *menziesii* (Hooker) Calder et Roy L. Taylor) of western North America. The fossil is different from *S. salicifolia* Linnaeus of southern Europe to Asia by the entire-margined lower part of the lamina.

Ulmaceae Mirbel

Ulmus Linnaeus

Ulmus carpinoides Göppert

Fig. 5b

1855 *Ulmus carpinoides* Göppert, p. 28, pl. 13, figs. 4–6

Material: SF.B 11759, 12076, 12077, 12085, 12102.

Description: Leaves simple, petiolate, petiole 3 and > 3 mm long, lamina ovate, > 30 mm long, 22–60 mm wide, margin double serrate, teeth short, apically curved, venation craspedodromous, primary vein straight, strong, secondary veins densely spaced, in 12–22 pairs, basally departing at wide, higher up at steeper angles, subparallel, tertiary veins very thin, reticulate between secondary veins.

Fig. 5 **a** *Ulmus pyramidalis* Göppert., complete leaf, SF.B 12101, 10 mm. **b** *Ulmus carpinoides* Göppert, complete leaf, SF.B 12077, 10 mm. **c** *Zelkova zelkovifolia* (Unger) Bůžek et Kotlaba, foliage shoot, SF.B 12016, 10 mm. **d** *Zelkova zelkovifolia* (Unger) Bůžek et Kotlaba, complete leaf, SF.B 12018, 10 mm

Remarks: Specimens of this kind of elm foliage from our collection of the Frankfurt flora fall within the morphological variability of *Ulmus carpinoides* described from the late Miocene locality Sośnica. The leaves at Sośnica are accompanied by two kinds of fruits, one ascribed to *U. pyramidalis* (see below) and another one, more rounded, corresponding to the living *U. campestris* Linnaeus (Z. Kvaček, personal

observation). The latter fruit type may belong to the foliage of the fossil species *U. carpinoides*.

Ulmus pyramidalis Göppert

Fig. 5a

1855 *Ulmus pyramidalis* Göppert, p. 28, pl. 13, figs. 10–12

1839 *Ulmus longifolia* Unger; Mädlar, p. 86, pl. 8, fig. 1

Material: SF.B 11781, 12093, 12097, 12101.

Description: Leaves simple, shortly petiolate, petiole 2–6 mm long, lamina lanceolate, 30–50 mm long, 6–13 mm wide, margin double serrate, teeth short, apically curved, venation craspedodromous, primary vein straight, strong, secondary veins densely arranged in 20 pairs, basally departing at wide angles, higher up at moderate angles, subparallel, tertiary veins thin, sinuous and densely arranged between secondaries.

Remarks: Similar fossil leaves have been ascribed to *Ulmus pyramidalis* from the late Miocene locality Sošnica and many other sites in the European Miocene (for synonyms, see Bůžek 1971). In the early Miocene flora of northern Bohemia, this foliage is accompanied by long-stalked samaras with a calyx remain above the stalk base (Bůžek 1971). The modern *U. americana* Linnaeus or *U. alata* Michaux from North America have been indicated as the nearest living species but they differ in the morphology of the fruits (position of the calyx).

Zelkova Spach

Zelkova zelkovifolia (Unger) Bůžek et Kotlaba

Fig. 5c, d

1845 *Ulmus zelkovifolia* Unger, pl. 24, figs. 9–13 (non fig. 7)
1939 *Zelkova ungeri* Kováts; Mädlar, p. 88, pl. 8, figs. 3–5
1963 *Zelkova zelkovifolia* (Unger) Bůžek et Kotlaba in Kotlaba, p. 59, pl. 3, figs. 7–8

Material: Original material of Mädlar (1939) V. 17173, V.26383, V.25384 and Stockholm S127818, new slides at SF.B 11986, 12004, 12016, 12018, 12049, 12062.

Remarks: Leaves and foliage shoots listed above correspond in leaf morphology to the type material of *Ulmus zelkovifolia* (i.e. *Zelkova zelkovifolia*) from Parschlug and other sites in the European Neogene. They are well comparable with some of the relictual modern species distributed in the Caucasus and south of the Caspian Sea and in southern Europe (Denk and Grimm 2005).

Fagaceae Dumortier

Fagus Linnaeus

Fagus kraeuselii Kvaček et Walther

Fig. 6b, c

1939 *Fagus ferruginea* Aiton *fossilis* Nathorst; Mädlar, p. 83, pl. 7, figs. 21, 22

1939 *Fagus decurrens* Reid; Mädlar, p. 84, pl. 7, figs. 28, 29

1991 *Fagus kraeuselii* Kvaček et Walther, p. 488, pls. 19–20, text-fig. 11b

2001 *Fagus kraeuselii* Kvaček et Walther; van der Burgh, p. 290, pl. 2, figs. 3–6, 8–9

2004 *Fagus haidingeri* Kováts; Denk, p. 11, pro parte, figs. 13B, G, 14D, E, M

Material: Numerous leaf compressions including the holotype SF.B 1197 and the paratypes SF.B 11902–11903, epidermal preparations KN 1/89–KN 7/89 (MMG), one leaf compression at Stockholm (S127837).

Description: For detailed description and synonymy, see Kvaček and Walther (1991) and Denk (2004).

Remarks: According to Kvaček and Walther (1991) and van der Burgh (2001), only biometrical differences have been detected between foliage of the Pliocene populations of *Fagus kraeuselii* and the late Miocene *F. menzelii* Kvaček et Walther and *F. silesiaca* Walther et Zastawniak. According to Denk (2004), late Miocene and Pliocene *Fagus* foliage previously assigned to various fossil species (*F. pliocaenica* Saporta, *F. kraeuselii*, *F. silesiaca*) should be included within *F. haidingeri* Kováts described from upper middle Miocene deposits of Hungary. Mädlar (1939) compared two fossil species of *Fagus* from Frankfurt to the modern North American *F. grandifolia* Ehrhart (as *F. ferruginea* Aiton) and to the Eurasian *F. sylvatica* Linnaeus and *F. crenata* Blume (as *F. sieboldi* Siebold et Zuccarini). According to Denk (2004), the closest similarity of the Frankfurt specimens is with the modern East Asian *F. crenata* Blume and *F. hayatae* Palibin ex Hayata.

Castanea Miller

Castanea sp.

Figs. 6a and 17f, g

1983 *Castanea* cf. *sativa* Miller sensu Hummel, p. 29, pl. 14, figs. 1–3a, pl. 15, figs. 1–5, text-figs. 12.1–15, 13.1, 14.1

Material: SF.B 11836, cuticle preparations SF.B 11836.1–2.

Description: Leaf fragment, petiolate, petiole > 20 mm long, lamina > 60 mm long, > 20 mm wide, base obtuse to shallowly cordate, primary vein straight and strong, secondary venation craspedodromous/semicraspedodromous, secondary veins evenly spaced, straight, ending in a bristle tooth, tertiary veins perpendicular to secondary veins, branching or more rarely percurrent, marginal (fimbrial) vein present. Cuticles extremely thin, adaxial not preserved, abaxial on veins with narrow straight-walled cells, unspecialised cells polygonal with anticlinal walls straight to slightly curved, stomata anomocytic, seen as elliptical guard cell pairs 25 µm long and 17 µm wide, ledges broad, but not thickened, pore narrow elliptical, 12 µm × 10 µm in size, solitary trichome bases ca. 15 µm in diameter with asymmetrical attachment of distal gland.

Remarks: The fragmentary specimen investigated agrees in the details of marginal venation and its epidermal anatomy with the material from the Pliocene site Ruszów, Poland, assigned to *Castanea* cf. *sativa* Miller (Hummel 1983).

◀ **Fig. 6** **a** *Castanea* sp., fragmentary leaf with long petiole, SF.B 11836, 10 mm. **b** *Fagus kraeuselii* Kvaček et Walther, complete leaf, SF.B 11907, 10 mm. **c** *Fagus kraeuselii* Kvaček et Walther, complete leaf, SF.B 11963, 10 mm. **d** *Quercus* sp., incomplete leaf, SF.B 11643, 10 mm. **e** *Quercus* sp., detail of leaf lamina, SF.B 11643, 5 mm. **f** *Quercus roburoides* Gaudin sensu Erw. Knobloch, lobate leaf, SF.B 11805, 10 mm. **g** *Quercus roburoides* Gaudin sensu Erw. Knobloch, lobate leaf, SF.B 11831, 10 mm. **h** *Quercus roburoides* Gaudin sensu Erw. Knobloch, lobate leaf, SF.B 11824, 10 mm. **i** *Quercus pseudocastanea* Göppert sensu Walther et Zastawniak, lobate leaf, SF.B 11834, 10 mm. **j** *Quercus roburoides* Gaudin sensu Erw. Knobloch, lobate leaf, SF.B 11843, 10 mm

Mädler (1939), pl. 7, figs. 19, 20) figured two specimens as *Castanea* sp. These specimens are very fragmentary and do not show much venation details. They are, however, more similar to the type of *Quercus* foliage described below as aff. *Q. kubinyi* (Kováts ex Ettingshausen) Czecczott.

Quercus Linnaeus

aff. *Quercus kubinyi* (Kováts ex Ettingshausen) Czecczott
Fig. 7a

1852 *Castanea kubinyi* Kováts, Ettingshausen, p. 6, pl. 1, fig. 12

1939 *Castanea* sp.; Mädler, p. 79, pl. 7, figs. 19, 20

1951 *Quercus kubinyi* (Kováts ex Ettingshausen) Czecczott, p. 392, fig. 7

Material: SF.B 11844a.

Description: Leaf fragment, margin regularly sharply dentate, teeth long acuminate, ending in a bristle, sinuses rounded, venation craspedodromous, primary vein stout, secondary veins simple, departing from primary vein at an angle of 60°, straight, marginal vein weakly developed, cuticle not accessible.

Remarks: The exact botanical affinity of this specimen is difficult to establish without information about the epidermal structure. Nevertheless, the marginal venation suggests *Quercus* rather than *Castanea* (for details, see Hummel 1983).

Quercus roburoides Gaudin sensu Erw. Knobloch
Figs. 6f–h, j and 17h

1859 *Quercus roburoides* Gaudin in Gaudin and Strozzi, p. 44, 58, pl. 3, fig. 14

1908 *Quercus robur* Linnaeus *pliocenica* Engelhardt in Engelhardt and Kikelin, p. 234, pro parte, pl. 28, fig. 18a

1939 *Quercus sessiliflora* Salisbury *fossilis* sensu Mädler, p. 78, pro parte, pl. 7, fig. 18

1998 *Quercus roburoides* Gaudin; Knobloch, p. 32, pl. 6, fig. 4, pl. 12, figs. 1–3, pl. 13, figs. 1–3, pl. 14, figs. 1–2, pl. 17, fig. 4

Material: SF.B 11805, 11824, 11831, 11842, 11843, cuticle preparations SF.B 11805.1–2.

Description: Leaves long petiolate, lamina elliptic to obovate, margin distinctly lobate, lobes rounded, more than six on each side, sinuses rounded, venation craspedodromous, primary vein stout, secondary veins simple, originating at an angle of 60°, straight, marginal vein weakly cuticle features similar in structure to the following fossil species.

Remarks: These leaves are closely similar to the modern *Q. petraea* (Mattuschka) Lieblein and allied taxa (*Q. dalechampii* Tenore, *Q. iberica* Steven ex M. Bieberstein, *Q. dshorochensis* K. Koch).

Quercus pseudocastanea Göppert sensu Walther et Zastawniak

Figs. 6i and 17i

1908 *Quercus robur* Linnaeus *pliocenica* Engelhardt in Engelhardt and Kikelin, p. 234, pl. 28, fig. 18b–k

1939 *Quercus sessiliflora* Salisbury *fossilis* Mädler, p. 78, pro parte, pl. 7, fig. 17

1991 *Quercus pseudocastanea* Göppert sensu Walther et Zastawniak, p. 169, pro parte, pl. 2, figs. 2–3, pl. 3, figs. 1–6, text-figs. 8.2–5, 7

Material: SF.B 11786, 11818, 11827, 11834, cuticle preparations SF.B 11786.1–3.

Description: Leaves long petiolate, lamina elliptic to obovate, margin distinctly lobate, lobes rounded to acute, venation craspedodromous, primary vein stout, secondary veins simple, originating at an acute angle, straight. Abaxial cuticle smooth, delicate, unspecialised cells not visible in the preserved cuticle structure, stomata anomocytic (?), uniformly sized, 25 µm long, 15–20 µm wide, pore narrow elliptic, short, stellate trichomes mostly four-armed, rarely encountered on veins, glandular trichomes with serial base, dense, occasionally in pairs, basal cell cylindrical, 12 µm in diameter, with attached short remain of distal part, simple rounded trichome bases 10 µm in diameter with thickened margin, scattered on veins.

Remarks: According to Knobloch (1998) and Worobiec and Szykiewicz (2016), *Quercus pseudocastanea* differs from *Q. roburoides* by acute lobes. The cuticle structure, which is the same for both forms, does not support such a distinction and hence it may be reasonable to maintain a broad concept of fossil roburoid oaks (Iljinskaya in Takhtajan 1982; van der Burgh 2001).

Quercus praecastaneifolia Erw. Knobloch
Figs. 7b–f and 17j

? 1964 *Quercus kodorica* Kolakovskii, p. 84, pro parte, pl. 29, fig. 1

1991 *Quercus pseudocastanea* Göppert sensu Walther et Zastawniak p. 169, pro parte, pl. 2, figs. 5–6, text-figs. 8.1, 8.6

◀ **Fig. 7** **a** aff. *Quercus kubinyii* (Kováts ex Ettingshausen) Czecczot, fragmentary leaf, SF.B 11844a, 10 mm. **b** *Quercus praecastaneifolia* Erw. Knobloch, complete leaf, SF.B sn11, 10 mm. **c** *Quercus praecastaneifolia* Erw. Knobloch, incomplete leaf, SF.B 11844b, 10 mm. **d** *Quercus praecastaneifolia* Erw. Knobloch, incomplete leaf, SF.B 11855, 10 mm. **e** *Quercus praecastaneifolia* Erw. Knobloch, complete leaf, SF.B 11850, 10 mm. **f** *Quercus praecastaneifolia* Erw. Knobloch, complete leaf, SF.B 11845, 10 mm

1998 *Quercus praecastaneifolia* Erw. Knobloch, p. 30, pl. 13, fig. 4, pl. 15, figs. 1–6, text-fig. 11a–b

Material: SF.B 11790, 11844b, 11845, 11850, 11855, sn11, cuticle preparations SF.B 1179.1, sn.11.1–2.

Description: Leaves shortly petiolate, lamina narrow obovate, apex bluntly acute, base shortly cuneate to rounded to shallowly subcordate, auriculate, margin regularly shallowly lobate with up to 16 lobes on each side of lamina, lobes blunt or indistinctly mucronulate, sinuses rounded, venation craspedodromous, primary vein straight, secondary veins in up to 18 pairs, regularly spaced, pinnate, adaxial cuticle medium thick, smooth, unspecialised cells polygonal, straight-walled, abaxial cuticle thin, smooth, unspecialised cells not well discernible, stomata anomocytic, elliptic, 20 µm long, 15 µm wide, pore short, slit-like, stellate trichomes scattered, two- to eight-armed, bases of glandular trichomes on veins, rare.

Remarks: According to Uzunova and Palamarev (1993), species of *Quercus* section *Quercus* (white oaks; Denk et al. 2017) have anomocytic stomata, while sections *Ilex* and *Cerris* are characterised by cyclocytic stomata. If this is a consistent feature, the leaves at hand would belong to white oaks. The narrow elongated, auriculate leaf base, rounded sinuses between the teeth, and absence of bristle-like extensions of the secondary veins also are suggestive of white oaks rather than section *Cerris*. Specifically, the investigated leaves have various features typical of white oaks from East Asia (e.g. *Q. griffithii* Hook.f. and Thomson ex Miquel, *Q. aliena* Blume, *Q. dentata* Thunberg in Murray; [Supplementary material](#) File 3). Knobloch (1998) compared such leaves from the Pliocene locality Willershausen with the modern *Q. castaneifolia* C.A. Meyer and established a new species *Q. precastaneifolia*. Most probably, this fossil species belongs to the white oaks and represents an extinct Pliocene species that did not survive into modern times.

Quercus sp.

Figs. 6d, e and 17k

Material: SF.B 11643, cuticle preparations SF.B 11643.1–2.

Description: Leaf incomplete, short petiolate, petiole 4 mm long, proximal part conspicuously dilated, only lower part of lamina preserved, entire-margined, 16 mm wide, incomplete length 47 mm, on one side with two shallow lobes giving the margin an undulating appearance, venation brochidodromous,

primary vein slightly bent, secondaries irregularly spaced, departing from primary vein at angles of 35–40–50°, partly with single intersecondaries perpendicular to primary vein, tertiary veins mixed percurrent, exterior tertiaries looped, areolation well developed, adaxial cuticle delicate, ordinary cells polygonal, straight-walled, solitary rounded trichome bases, abaxial cuticle smooth, very thin, ordinary cells not recognisable, stomata seen as elliptical outlines 15 µm long with very narrow stomatal ledges, appearing anomocytic, bases of serial glandular trichomes thin-walled, 12 µm in diameter with incomplete terminal parts up to 25 µm long and pear-like basal cells dispersed among stomata.

Remarks: The leaf is very delicate, characteristic of deciduous foliage. The glandular indumentum is comparable with serial trichomes in the Fagaceae. The morphology suggests an aberrant leaf form of *Quercus robur* Linnaeus. Similar leaf forms, but with longer petioles, have been recovered in Neogene deposits of northern Greece, Vegora mine (Kvaček et al. 2002, pl. 14, fig. 5) and assigned to *Q. pseudocastanea* Göppert. The structure of the thin cuticle with only bases of glandular trichomes matches the above-mentioned leaf compressions assigned to *Quercus praecastaneifolia*. Such narrow leaf forms are produced by oak cultivars, such as *Quercus petraea* “laciniata” but also occur as variants of *Q. infectoria* Oliver (var. *pfaeffingeri* (Kotschy ex Tchichatcheff) Jamzad et Panahi). Alternatively, similar leaf forms may be encountered in North American deciduous swamp oaks of sect. *Lobatae*.

Juglandaceae DC. ex Perleb

Carya Nuttall

Carya sp.

Fig. 8a, b

1908 *Carya* sp.; Engelhardt and Kinkel, p. 241, pl. 31, fig. 7

1908 *Pterocarya denticulata* (Weber) Heer; Engelhardt and Kinkel, p. 242, pl. 31, fig. 8a–d

1939 *Pterocarya denticulata* (Weber) Heer; Mädler, p. 57, pl. 6, figs. 16–19 (? non fig. 3, fruit)

Material: SF.B 11672 11673, 11675, 11676, 11677, 11678, 11679, 11681, 11686, 11691.

Description: Leaflets narrow to broadly elliptic, sharply simple serrate, secondary venation brochidodromous with additional loops.

Remarks: See below, for *Pterocarya*.

Pterocarya Kunth

Pterocarya paradisiaca (Unger) Iljinskaya

Fig. 8c

Material: SF.B 11680, 11684, 11690, 11692, 11693. 11696, 11698.

◀ **Fig. 8** **a** *Carya* sp., incomplete leaflet, SF.B 11690, 10 mm. **b** *Carya* sp., complete leaflet, SF.B 11681, 10 mm. **c** *Pterocarya paradisiaca* (Unger) Iljinskaya, complete leaflet, SF.B 11623, 10 mm. **d** *Betula similis* (Göppert) Zastawniak et Walther, complete leaf, SF.B 11805, 10 mm. **e** *Betula similis* (Göppert) Zastawniak et Walther, incomplete leaf, SF.B 11792, 10 mm. **f** *Betula longisquamosa* Mädlar, fruit, SF.B 11809, 10 mm. **g** *Alnus gaudinii* (Heer) Erw. Knobloch et Kvaček, incomplete leaf, SF.B 11762, 10 mm. **h** *Alnus gaudinii* (Heer) Erw. Knobloch et Kvaček, complete leaf, SF.B 11760, 10 mm. **i** *Carpinus grandis* Unger, complete leaf, SF.B 11754, 10 mm. **j** *Carpinus grandis* Unger, complete leaf, SF.B 11734, 10 mm. **k** *Carpinus grandis* Unger, fruit, SF.B 11747, 10 mm. **l** *Carpinus grandis* Unger, fruit, SF.B 11714, 10 mm

Description: Leaflets asymmetrical, slender at base, bluntly simple serrate, secondary venation brochidodromous.

Remarks: The differences between foliage of *Carya*, *Cyclocarya* Iljinskaja and *Pterocarya* are difficult to establish. A more exact identification requires epidermal details of every specimen (see Kvaček et al. 2008). However, the blunt, simple serrate margin of the leaflets included here indicates that they belong to *Pterocarya*.

Betulaceae Gray

Betula Linnaeus

Betula similis (Göppert) Zastawniak et Walther

Figs. 8d–f and 17l–m

1855 *Alnus similis* Göppert, p. 13, pl. 4, fig. 5

1998 *Betula similis* (Göppert) Zastawniak et Walther, p. 103, pl. 4, fig. 5, pl. 5, figs. 1–7, pl. 6, figs. 6–8, text-figs. 2/8, 11–12, 3/5, 8, 10/1–13, 13/12–13

Material: SF.B 11784, 11785, 11787, 11792, 11800, 11805, 11806 (leaves).

Description: Leaves petiolate, lamina ovate, 45–70 mm long, 23–55 mm wide, base cuneate, apex acute, margin simple, rarely double serrate, teeth eglandular, narrow acute to apiculate, venation craspedodromous, primary vein straight, secondary veins straight, in five to eight pairs, agrophic lateral veins single or several, tertiary veins distinct, epidermal structure (no. SF.B 11806) of adaxial cuticle distinct, ordinary cells straight-walled, 20–50 µm in diameter, dispersed simple trichome bases on veins, abaxial cuticle thin, ordinary cells straight-walled, 15–25 µm in diameter, stomata anomocytic, of different size, 12–25 µm long, 10–15 µm wide, solitary polycellular bases of glands on veins both abaxially and abaxially.

Remarks: Leaves co-occur with fruit bracts of *B. longisquamosa* Mädlar (Fig. 8f). As stated by Hummel (1991) the fossil species is similar in epidermal structure to the modern *B. platyphylla* Sukaczew and corresponds to that described for *Betula plioplaptera* Hummel (1991) and *B. subpubescens* Göppert sensu Hummel (1991) from Ruszów. The epidermal structure is unknown from Göppert's type material from Sośnica (Zastawniak and Walther 1998), but a part of the specimens assigned to *Alnus adscendens* (Göppert) Zastawniak et Walther from the same site overlaps with *Betula similis*.

Alnus Miller

Alnus gaudinii (Heer) Erw. Knobloch et Kvaček

Fig. 8g, h

Material: SF.B 11760, 11762.

Description: Leaves long petiolate, petiole up to 20 mm long, lamina > 80 mm long, narrow ovate, 30–35 mm wide, rounded at base, apex not preserved, margin indistinctly serrate, venation semicraspedodromous–craspedodromous, primary vein straight, secondaries regularly spaced, mostly at an angle of 60°, in 7–10 pairs.

Remarks: Similar alder leaves are known from Oligocene to Pliocene strata of Central Europe. Among these are leaves from the Pliocene of Willershausen referred to as *Alnus* cf. *gaudinii* (Heer) Erw. Knobloch et Kvaček (Knobloch 1998, pl. 43, figs. 1–7) and the late Miocene flora of Kodor, Abkhazia (Kolakovskij 1964, as *Alnus agustifolia*). The nearest living relative for this fossil species is the Caucasian alder, *A. subcordata* C.A. Meyer that differs from the fossil species by slightly wider leaves.

Carpinus Linnaeus

Carpinus grandis Unger

Fig. 8i–l

1939 *Carpinus betulus* Linnaeus *fossilis* Engelhardt et Kinkel; Mädlar, p. 77, pl. 7, figs. 15–16

Material: A few selected most characteristic specimens SF.B 11708, 11709, 11710, 11711, 11732, 11734, 11745, 11748, 11750, 11752, 11753, 11754, 11774, 11776.

Description: Leaves petiolate, lamina elliptic to ovate, finely and sharply double serrate, base cuneate to cordate, apex acute, venation craspedodromous, secondary veins dense, regularly spaced, departing from primary vein at moderate angles. For details, see Mädlar (1939).

Remarks: The foliage co-occurs with fruits of the *Carpinus betulus* type (SF.B 11714, 11718, 11721, 11726, 11747). The nearest living relative is *Carpinus betulus* Linnaeus distributed in the temperate zone of Europe to Iran.

Carpinus cf. *uniserrata* (Kolakovskij) Ratiani

Fig. 9a

? 1955 *Carpinus cuspidens* (Saporta) Kolakovskij var *uniserrata* Kolakovskij, p. 232, pl. 4, figs. 6–7

? 1964 *Carpinus uniserrata* (Kolakovskij) Ratiani ex Kolakovskij, p. 65, pl. 19, figs. 7–14

Material: SF.B 11728, 11731.

Description: Leaves short petiolate, blade narrow ovate, more than 60 mm long, ca. 20 mm wide, apex long acute, base cuneate,

◀ **Fig. 9** **a** *Carpinus* cf. *uniserrata* (Kolakovskij) Ratiani, complete leaf, SF.B 11731, 10 mm. **b** *Corylus kolakovskiyi* Budantsev, complete leaf, SF.B 11751, 10 mm. **c** *Corylus kolakovskiyi* Budantsev, incomplete leaf, SF.B 11757, 10 mm. **d** *Trichosanthes* sp., complete leaf, SF.B 12226, 10 mm. **e** *Salix lavateri* A. Braun sensu Hantke, incomplete leaf, SF.B 11633, 10 mm. **f** *Salix lavateri* A. Braun sensu Hantke, complete leaf, SF.B 11654, 10 mm. **g** *Populus canescens* Erw. Knobloch, complete leaf, SF.B 11532, 10 mm. **h** *Populus canescens* Erw. Knobloch, complete leaf, SF.B 11537, 10 mm. **i** *Populus balsamoides* Göppert, complete leaf, SF.B 11520, 10 mm

margin sharply double serrate, venation craspedodromous, primary vein straight, secondary veins > 12 pairs, steep.

Remarks: Knobloch (1998) stated that this type of foliage resembles *Ostrya* Scop. We agree with Knobloch (1998), who described similar leaf forms from the Pliocene of Willershausen and considered them belonging to the genus *Carpinus*. The modern hornbeam *C. caroliniana* Walter (syn. *C. americanus* Michxaux) produces similar but wider and coarsely serrate leaves.

Corylus Linnaeus

Corylus kolakovskiyi Budantsev

Fig. 9b, c

Fig. 10 **a** *Populus gregorii* Erw. Knobloch, incomplete leaf, SF.B 11589, 10 mm. **b** *Populus gregorii* Erw. Knobloch, fragmentary leaf, SF.B 11591, 10 mm. **c** *Populus populina* (Brongniart) Erw. Knobloch, complete leaf, SF.B 11598, 10 mm. **d** *Populus populina* (Brongniart) Erw.

Knobloch, incomplete leaf, SF.B 11551, 10 mm. **e** *Celtis trachytica* Ettingshausen, incomplete leaf, SFB. 12125, 10 mm. **f** *Celtis trachytica* Ettingshausen, incomplete leaf, SF.B 12118, 10 mm

1982 *Corylus kolakovskiy* Budantsev in Takhtajan, p. 173, pl. 96, figs. 3–4

Material: SF.B 11751, 11755 11757, 11763.

Description: Leaves long petiolate, lamina broadly obovate, up to 60 mm long, 40 mm wide, margin finely double serrate, base cordate, apex bluntly cuneate, secondary venation craspedodromous, primary vein straight, secondary veins up to eight pairs, straight, basally numerous abmedial veins, tertiary veins slightly oblique, dense, reticulate.

Remarks: The original material of *Corylus kolakovskiy* was described from the Pliocene of Duab and compared with *C. avellana* (Kolakovskij 1952). According to Budantsev (in Takhtajan 1982), foliage of this fossil species is morphologically more similar to the living *Corylus maxima* Miller due to a less prominently lobed margin. The same leaf morphotype was determined as *Corylus avellana* Linnaeus *fossilis* from the Pliocene of Willershausen (Knobloch 1998, p. 43, pl. 5 fig. 10, pl. 19, figs. 2–3, pl. 22, fig. 10, pl. 23, fig. 4, pl. 25, figs. 1–2, 5).

Cucurbitaceae Jussieu
Trichosanthes Linnaeus
Trichosanthes sp.
 Figs. 9d and 17n

? 1939 *Magnolia moenana* Mädlar, p. 96, pl. 1, figs. 7–8, text-fig. 29
 ? 1939 *Acer palaeo-miyabei* Mädlar, p. 117, pro parte, pl. 9, fig. 17
 ? 1939 *Acer integerrimum* Viviani sensu Mädlar, p. 118, pro parte, pl. 9, fig. 18
 2008 *Trichosanthes* sp.; Kvaček, Teodoridis and Gregor, p. 31, pl. 9, figs. 13–16, pl. 10, figs. 1–3, pl. 20, figs. 12–14

Material: SF.B 12191, 12226, cuticle preparations SF.B 12191.1–2.

Description: Leaves trilobate (to pentalobate), lobes entire-margined. Fragments of adaxial cuticle revealing thin, straight-walled unspecialised cells; the structure of the abaxial cuticle not well discernible, thin cuticle on its surface crenulate–striate, showing indistinct, tiny, rounded stomata 10–15 µm in diameter, thick-walled simple trichomes 120–380 µm long with bulbous base 35–45 µm in diameter, distributed across the abaxial leaf surface.

Remarks: Mädlar (1939) described similar massive trichomes on a leaf fragment, which he interpreted as serial trichomes. He considered the fragment to belong to *Magnolia*. Similar hairy leaf fossils have previously been recovered from Pliocene deposits of Auenheim and were identified as *Trichosanthes* (Kvaček et al. 2008).

Salicaceae Mirbel
Salix Linnaeus

Salix lavateri A. Braun sensu Hantke
 Fig. 9e, f

1851 *Salix lavateri* A. Braun, p. 78
 1908 *Salix denticulata* Heer; Engelhardt and Kinkel, p. 228, pl. 28, figs. 2a, b (? Non “Knospenschuppen” 3–4)
 1939 *Salix denticulata* Heer; Mädlar, p. 52, pl. 5, fig. 15 (? non fruits 16–17)
 1954 *Salix lavateri* A. Braun; Hantke, p. 55, pl. 5, figs. 2–16

Material: Only newly recovered leaves; SF.B 11602, 11604, 11609, 11619, 11616, 11623, 11633, 11635, 11637, 11645, 11646, 11649, 11651, 11652, 11656, 11654 (cf.), cuticle preparations SF.B 11623.1–3.

Description: Adaxial cuticle smooth, on veins slightly striate, unspecialised cells polygonal, straight-walled, ca. 25–35 µm in diameter, solitary brachyparacytic stomata and simple rounded trihome bases near margin; abaxial cuticle smooth, at places slightly striate, anticlinal walls of unspecialised cells rarely seen, straight, stomata brachyparacytic, guard cell pairs narrow elliptic, uniformly sized, 15–20 µm long, 10 µm wide, solitary simple trichome bases.

Remarks: The new material belongs to the same morphotype as described by Mädlar (1939, as *Salix denticulata*). The single leaf epidermis studied matches only a part of the material of *Salix* from Auenheim, namely the specimens that almost lack the wax cover abaxially (Kvaček et al. 2008, p. 32, as *Salix* sp.).

Populus Linnaeus
Populus balsamoides Göppert
 Figs. 9i and 18d, e

1855 *Populus balsamoides* Göppert, p. 23, pl. 15, figs. 5–6
 1939 ? *Populus* sp. cf. *nigra* L.; Mädlar, p. 52, pl. 5, figs. 18–19

Material: Numerous newly recovered compressions in glass preparations, > 15 leaves including fragments; selected specimens SF.B 11508, 11509, 11511, 11515, 11520, 11524, 11525, 11526, cuticle preparations SF.B 11670.1–2.

Description: Leaves long petiolate, lamina ovate, margin glandular crenulate. A single leaf compression yielded only cuticle of the abaxial side, cuticle very thin, fragmentary, unspecialised cells with curved anticlinal walls, stomata brachyparacytic, guard cell pairs elliptic, 17–25 µm long, 12–15 µm wide, ledges slightly thickened, reaching almost to poles, pore narrow to widely spindle-shaped, solitary trichome bases simple rounded, on veins.

Remarks: The cuticle structure matches the material described from the Pliocene of Auenheim and identified as *Populus* cf. *balsamoides* (Kvaček et al. 2008). This very common fossil poplar species requires revision of the type material from the late Miocene site Sośnica. Iljinskaja (2005) suggested close similarities of this

fossil species with the modern *P. tibetica* Thomson ex Kam.

Populus populina (Brongniart) Erw. Knobloch
Fig. 10c, d

1822 *Phyllites populina* Brongniart, p. 237, pl. 14, fig. 4
1964 *Populus populina* (Brongniart) Erw. Knobloch, p. 601
1988 *Populus populina* (Brongniart) Erw. Knobloch, p. 16, pl. 9, figs. 2, 6, pl. 13, figs. 6–8

Material: SF.B 11531, 11535, 11536, 11545, 11550, 11551, 11552, 11553, 11554, 11555, 11556, 11557, 11560, 11563, 11564, 11565, 11566, 11568, 11569, 11571, 11572, 11573, 11581, 11554, 11555, 11556, 11557, 11553, 11552, 11564, 11571, 11560, 11568, 11569, 11563, 11566, 11580, 11581, 11598, 11600, 11601.

Description: See Knobloch (1964, 1988).

Remarks: The above listed specimens include morphotypes matching the type specimen of Brongniart's *Phyllites populina*. The cuticle structure of specimens was not accessible.

Populus gregorii Erw. Knobloch
Fig. 10a, b

1998 *Populus gregorii* Erw. Knobloch, p. 52, pl. 27, figs. 1–4, 6, text-fig. 18

Material: SF.B 11587, 11589, 11591, 11592, 11595, 11597.

Description: Leaves long petiolate, lamina ovate, margin from the base upwards bluntly and regularly dentate.

Remarks: Similar morphotypes have been assigned to *Populus tremula pliocenica* Saporta from the Pliocene locality of Reuver (Laurent and Marty 1923, p. 13, pl. 2, figs. 4–9).

Populus canescentoides Erw. Knobloch
Fig. 9g, h

1998 *Populus canescentoides* Erw. Knobloch, p. 51, pl. 27, figs. 5, 7, pl. 29, figs. 7, 9

Material: SF.B 11530, 11532, 11534, 11537, 11538, 11539, 11542, 11543, 11544, 11546, 11547, 11548, 11549, 11558, 11567, 11578, 11593.

Description: Leaves long petiolate, lamina broadly ovate to narrow ovate, in upper part shallowly widely lobate.

Remarks: This morphotype is similar in leaf shape and margin to the Pliocene population from Reuver (Laurent and Marty 1923, p. 13, pl. 3, figs. 3, 5–6 assigned to *Populus alba pliocenica*).

Cannabaceae Martinov
Celtis Linnaeus

Celtis trachytica Ettingshausen
Fig. 10e, f

1853 *Celtis trachytica* Ettingshausen, p. 801, pl. 1, fig. 7

Material: SF.B 11562, 12115, 12118, 12124, 12125.

Description: Leaf short petiolate, petiole 5–8 mm long, lamina 45 to > 80 mm long, 20–40 mm wide, base rounded to acute, slightly asymmetric, margin sparsely toothed, venation triveined, primary vein and two lateral veins originating from leaf base, lateral veins similar to secondary veins, secondary venation brochidodromous, departing in a steep angle from primary vein, bent, additional loops formed by abmedial veins, small side veins from secondary and abmedial veins entering the fine teeth, tertiary veins perpendicular to secondary veins, percurrent or branched.

Remarks: Kutuzkina (in Takhtajan 1982) considered this fossil species with rounded leaf base and typical of the late Miocene of Europe as distinct from *C. japeti* Unger, which is more common in middle Miocene strata.

Sapindaceae Jussieu
Acer Linnaeus

Acer dombeyopsis Kvaček, Teodoridis et Denk sp. nov.
Figs. 11a, b and 18f, g

Material: SF.B 12186, 12202, 12204, 12211, 12220, 12237, 12238, 12270, cuticle preparations SF.B 12211.1–3.

Holotype selected here: SF.B 12211 (fig. 11a), cuticle preparation SF. B 12211.1.

Derivatio nominis: Referring to the leaf morphological similarity with the fossil genus *Dombeyopsis* Unger.

Description: Leaves palmately shallowly trilobed, entire-margined (or rarely with a few sharp teeth on lobes). Areoles without free-ending veinlets (sample SF.B. 12211); adaxial cuticle smooth, thin, reflecting wavy anticlines of ordinary cells, ordinary cells 20–50 µm in diameter, abaxial cuticle thin, ordinary cells ca. 20 µm in diameter, stomata rounded, anomocytic (to cyclocytic), 20–25 µm in diameter, stomatal ledges broad, pore short, 10 µm long, simple trichomes 150–200 µm long very sparsely dispersed over the whole abaxial surface.

Remarks: *Acer dombeyopsis* imitates in its leaf anatomy and morphology some Hamamelidaceae (*Disanthus*, *Mytillaria*), but stomata are anomocytic and the general features of epidermal anatomy correspond to *Acer*. In its leaf morphology, *A. dombeyopsis* corresponds to *A. paxii* Franchet and *A. buergerianum* Miquel of the section *Pentaphylla* Hu et Cheng native in mountains of Yunnan and to *A. sterculiaceum* Wallich (Himalayas to East Asia) in the sect. *Lithocarpa* Pax (van Gelderen et al. 1994). A fragment of the same species showing similar epidermal patterns was described as *Acer integerrimum* (Viviani) Massalongo by Kvaček et al. (2008), p. 25, pl. 7, figs. 12–13, pl. 19, figs. 11–12) from the Pliocene flora of Auenheim.

◀ **Fig. 11** **a** *Acer dombeyopsis* Kvaček, Teodoridis et Denk sp. nov., incomplete leaf, SF.B 12211, 10 mm. **b** *Acer dombeyopsis* Kvaček, Teodoridis et Denk sp. nov., incomplete leaf, SF.B 12270, 10 mm. **c** *Acer* aff. *platanoides* Linnaeus, incomplete leaf, SF.B 12234, 10 mm. **d** *Acer integerrimum* (Viviani) Massalongo, incomplete leaf, SF.B 12243, 10 mm. **e** *Acer pyrenaicum* Rérolle, complete leaf, SF. B 12352, 10 mm. **f** *Acer subcampestre* Göppert, complete leaf, SF.B 12324, 10 mm. **g** *Acer viburnoides* Kvaček, Teodoridis et Denk sp. nov., complete leaf, SF.B 12210, 10 mm. **h** *Acer vitiforme* Kvaček, Teodoridis et Denk sp. nov., complete leaf, SF.B 12247, 10 mm. **i** *Acer vitiforme* Kvaček, Teodoridis et Denk sp. nov., complete leaf, holotype SF.B 12183, 10 mm

Acer aff. *platanoides* Linnaeus

Figs. 11c and 18k, l

Material: SF.B 12219, B12234, cuticle preparations SF.B 12219.1–2.

Description: Leaves simple, long petiolate, lamina palmately pentalobate; adaxial cuticle smooth to faintly striate, unspecialised cells 35–50 µm in diameter, anticlinal walls strongly zick-zack undulate; abaxial cuticle non-papillate, thin, smooth, strong trichomes on veins, stomata anomocytic, broadly elliptic to rounded, ca. 22 µm in diameter, stomatal ledges slightly thickened, pore broadly elliptic, simple trichomes ≥ 120 µm long, dispersed on veins.

Remarks: The examined pentalobate maple leaf compressions correspond in gross morphology as well as epidermal anatomy (SF.B 12219) to the modern *Acer platanoides* L. (Europe–Caucasus) and *Acer miyabei* Maximowicz (northern Japan), *Acer* sect. *Platanoidea* Pax. They differ from the fossil *A. protomiyabei* Endo (Miocene of Japan, Tanai 1983) by wider lobes. The epidermal anatomy of the latter is not known. Fossils with close relationships to the extant *A. platanoides* have only rarely been recorded in the fossil state. Fruits comparable with *A. platanoides* have been described from the Pliocene of Frankfurt/M. by Mädler (1939) as *A. platanoides* Linnaeus *fossilis*. For morphological comparisons of similar fossils from Asia, see Wolfe and Tanai (1987, pl. 61) and Tanai (1983), p. 301, 334, pl. 8, figs. 1, 3, text-fig. 3.28).

Acer pyrenaicum Rérolle

Fig. 11e

1884–1885 *Acer pyrenaicum* Rérolle, p. 386, pl. 12, figs. 2–6

Material: SF.B 12352, 12356, 12357, 12358, 12359, 12360.

Description: Leaves simple, broadly ovate to rarely sub-trilobate, long petiolate, petiole dilatated at base, 25–32 mm long, lamina 43–65 mm long, 38–55 mm wide, margin double crenate to bluntly dentate in upper two thirds, apex rounded to acute or rarely shortly acuminate, partly with two rounded lobes, base rounded to shallow cordate, venation palmate, craspedodromous to semicraspedodromous, three primary

veins, exceptionally five, primary vein stout, lateral primary and lower secondary veins departing at angles of 30–35°, higher secondary veins departing at wider angles, curved into marginal teeth, intersecondary veins rare, epimedial tertiary veins alternate percurrent, exterior tertiary veins variable.

Remarks: The foliage compressions assigned to *A. pyrenaicum* are variable in leaf shape from broadly elliptic to sub-trilobate, but quite characteristic in the dentition and venation patterns. Similar leaf fossils were rarely noted, partly together with fruits of the *Acer tataricum* type in the European Pliocene, e.g. at Lozenetz (Palamarev and Kitanov 1988, pl. 10, fig. 5, as *Acer tricuspidatum* A.Br. ex Agass. forma *productum* (A. Braun) Procházka et Bůžek) and Gurmen (Palamarev and Kitanov 1977, p. 17, text-fig. 1, as *Acer tataricum* Linnaeus *fossilis*) in Bulgaria (see Palamarev et al. 2005, p. 241). Similar morphotypes but differing in mostly broader sub-trilobate leaf lamina have been assigned to *Acer pyrenaicum* Rérolle from late Neogene sites in southern Europe (see Kvaček et al. 2002, p. 86). The epidermal structure obtained from morphologically similar leaf compressions from the Pliocene of Auenheim (Kvaček et al. 2008, as *Acer* cf. *tricuspidatum* Bronn forma *productum* (A. Braun) Procházka et Bůžek) deviates from the common epidermal structure of *Acer tricuspidatum*, which shows dense and thick-walled trichomes (cf. Walther 1972). The modern *Acer tataricum* Linnaeus subsp. *tataricum* of section *Ginnala* Nakai distributed in Eastern Europe to Caucasus and Turkey resembles this fossil species in leaf architecture. Typical foliage of *Acer tataricum* differs distinctly by the acuminate apex and the elongate elliptic form of the lamina. Since the fossil leaves are not preserved in physical connection with fruits, the affinities with modern maples are difficult to establish. Some more modern species (e.g. *A. pycnanthum* K. Koch from Japan or a doubtful hybrid *A. x schwerinii* Pax) may also produce similar foliage.

Acer subcampestre Göppert

Figs. 11f and 18h, i

1855 *Acer subcampestre* Göppert, p. 34, pl. 22, figs. 16–17

Material: SF.B 12198, 12209, 12213, 12324, cuticle preparations SF.B 12324.1–3.

Description: Leaves palmately tri- to pentalobate, petiolate, lamina chartaceous, 45–55 mm long, 60–80 mm wide, lobes acute, 16 to 30 mm wide, apically with shallow blunt teeth, basally shallow cordate, petiole thin, > 20 mm long, usually not preserved, venation palmate, three primary veins, straight craspedodromous, secondary veins and solitary intersecondaries semicraspedodromous, epimedial tertiaries mixed, areoles mostly without free-ending veinlets. Cuticles (investigated in SF.B 12324) extremely thin. Adaxial cuticle smooth to fine striate, ordinary cells polygonal, 25 µm in diameter; abaxial cuticle with straight-walled ordinary cells on veins, ca. 8 µm wide, 25 µm

◀ **Fig. 12** **a** *Aesculus hippocastanoides* Iljinskaja, complete leaflet, SF.B 12390, 10 mm. **b** *Aesculus hippocastanoides* Iljinskaja, incomplete leaflet, SF.B 12392, 10 mm. **c** *Aesculus hippocastanoides* Iljinskaja, complete leaflet, SF.B 12391, 10 mm. **d** “*Juglans*” *acuminata* A. Braun, incomplete leaflet, SF.B 11668, 10 mm. **e** “*Juglans*” *acuminata* A. Braun, complete leaflet, SF.B 11665, 10 mm. **f** *Hibiscus* sp., complete leaf, SF.B 12263, 10 mm. **g** *Hibiscus* sp., complete leaf, SF.B 12347, 10 mm. **h** aff. *Dombeyopsis lobata* Unger, complete leaf, SF.B 12194, 10 mm. **i** ? *Tilia* sp., isolated bracts, SF.B 12386, 10 mm

long; stomata anomocytic, elliptic to narrow elliptic, of different sizes, mostly 12 µm long and 7–10 µm wide, rarely larger, up to 28 µm long and 18 µm wide, stomatal ledges thin, forming short elliptic outer cavity, pore linear. Single peltate glands with polycellular heads on veinlets, solitary simple unicellular trichomes on thicker veins, no papillae observed.

Remarks: The leaf morphology of this fossil species is variable, as seen in the newly described type material of Sośnica (Walther and Zastawniak 2005) and in various late Miocene and Pliocene localities in Europe (Ströbitzer-Hermann and Kovar-Eder 2003). Leaf epidermal features of this species are here reported for the first time. *Acer subcampestre* is characterised by its very delicate cuticle, which is well distinguishable from the much tougher cuticles of *Acer tricuspidatum* Bronn, which is densely hairy on the abaxial leaf side (Walther 1972), and from similar maple species of sect. *Acer* with papillate abaxial cuticles. Among extant species of sect. *Platanoidea*, *A. campestre* L. has similarly arranged ordinary cells and stomata and differs in having few thick-walled simple non-glandular trichomes with thick finely granulate walls and polycellular glandular peltate trichomes, ca. 50 µm in diameter, on bi-triseriate stalks.

Acer integerrimum (Viviani) Massalongo
Figs. 11d and 20i, j

1833 *Acerites integerrima* Viviani, p. 131, pl. 11, fig. 6
1859 *Acer integerrimum* (Viviani) Massalongo; Massalongo and Scarabelli, p. 341, pl. 18, fig. 3

Material: SF.B 12243, 12298, cuticle preparation SF.B 12243.1.

Description: Leaf long petiolate, petiole 28 mm long, lamina preserved only in lower part, trilobate (?), shallow cordate, entire-margined, the preserved lobe acute. Adaxial cuticle reflecting unspecialised polygonal cells with straight to wavy anticlines, 25–35 µm in diameter; abaxial cuticle fragmentary, smooth showing anomocytic stomata irregularly orientated, rounded to broadly elliptic 15–20 (–26) µm with wide pore limited by thick stomatal ledges not reaching to the poles, simple smooth thin-walled trichomes 10 µm thick and up to 130 µm irregularly and sparsely distributed on the abaxial cuticle.

Remarks: Similar trilobate leaf forms of this maple species occur in the Miocene of Europe (e.g. in Senigaglia, Italy,

Massalongo in Massalongo and Scarabelli 1859, in the Most Basin, Procházka and Bůžek 1975, Kvaček et al. 2004, p. 131, fig. b), but usually with acuminate lobes. The cuticle structure is commonly not preserved because of its delicate nature.

Acer viburnoides Kvaček, Teodoridis et Denk sp. nov.
Figs. 11g and 18j

1939 *Acer brachyphyllum* Heer; Mädlar, p. 114, pl. 9, figs. 9–10

Material: SF.B 12210, cuticle preparations SF.B 12210.1–4.

Holotype here selected: Leaf compression between glass slides SF.B 12210 (fig. 11g).

Derivatio nominis: The species epithet refers to the resemblance of the leaf with *Viburnum opulus* L.

Description: Leaf simple, petiolate, petiole thin, lamina chartaceous, shallowly trilobate, apex broadly acute, margin shallowly bluntly simple dentate-lobed, venation basal actinodromous, midrib thin, only slightly thicker than secondaries, basal veins departing at an angle of 40°, higher secondary veins subparallel and widely irregularly spaced, simple, looping and curved along margin, tertiary veins irregularly reticulate. Adaxial and abaxial cuticles thin, adaxial cuticle faintly striate, unspecialised cells irregularly polygonal, 25–50 µm in diameter, with curved anticlinal walls, abaxial cuticle densely finely papillate, papillae granular, ca. 8 µm in diameter, papillae larger towards leaf margin, densely distributed on stomatal areas, forming rings around hardly visible elliptic stomata, stomata 15 µm long and 10 µm wide.

Remarks: The leaf compression corresponds in leaf morphology to *Acer* and *Viburnum*. *Acer obtusifolium* Sibthorp et Smith (eastern Turkey, Syria, and Lebanon), *Acer* sect. *Acer* is closely similar to the fossil species in leaf epidermal characteristics (Grimm et al. 2007) and in overall leaf shape but differs from the fossil species in its sub-entire margin. The previously applied species name *Acer brachyphyllum* Heer (Mädlar 1939, p. 114, pl. 9, figs. 9–10) is reserved for specimens that belong morphologically to *A. tricuspidatum* Bronn f. *brachyphyllum* (Heer) Procházka et Bůžek (1975, p. 28), although epidermal characters of the type specimens from the Sarmatian of Öhningen are not available. *Viburnum opulus* var. *opulus* and a closely related American species *V. trilobum* Marshall, often considered as *V. opulus* var. *americanum* Aiton imitate *Acer* in leaf morphology but clearly differ in epidermal anatomy (non-papillate, striate abaxial cuticle, a different kind of anomocytic stomata).

Acer vitiforme Kvaček, Teodoridis et Denk sp. nov.
Figs. 11h, i and 18m, n

Holotype: SF.B 12183 (fig. 11i), cuticle preparation SF.B 12183.1.

◀ **Fig. 13** **a** *Dicotylophyllum* sp. C, incomplete leaf, SF.B 12433, 10 mm. **b** *Dicotylophyllum* sp. D, complete leaf, SF.B 12440, 10 mm. **c** *Dicotylophyllum* sp. E, complete leaf, SF.B 12434, 10 mm. **d** *Dicotylophyllum* sp. F., incomplete leaf, SF.B 12435, 10 mm. **e** *Dicotylophyllum* sp. G, complete leaf, SF.B 12441, 10 mm. **f** *Dicotylophyllum* sp. H, leaf fragment, SF.B 12442, 10 mm. **g** *Dicotylophyllum* sp. I, leaf fragment, SF.B 12433, 10 mm. **h** *Dicotylophyllum* sp. J, leaf fragment, SF.B 12431, 10 mm. **i** *Dicotylophyllum* sp. K, leaf fragment, SF.B 12430, 10 mm. **j** *Dicotylophyllum* sp. L, incomplete leaf, SF.B 12437, 10 mm. **k** *Dicotylophyllum* sp. M, leaf fragment, SF.B 12156, 10 mm. **l** *Dicotylophyllum* sp. N, incomplete leaf, SF.B 12176, 10 mm. **m** *Dicotylophyllum* sp. O, complete leaf, SF.B 12180, 10 mm

Paratype: SF.B 12319, cuticle preparations SF.B 12319.1–4.

Other material: SF.B 12262, 12247, 12256, 12289, 12294, 12330.

Derivatio nominis: Referring to the morphological similarity of foliage in *Acer* and Vitaceae.

Diagnosis: Leaves simple, long petiolate, lamina broadly ovate, trilobate to shortly pentalobate, coarsely dentate, subcordate, slightly asymmetrical, adaxial cuticle faintly striate, ordinary cells polygonal, anticlinal walls straight to slightly bent, abaxial cuticle distinctly fine papillate, stomata cyclocytic, surrounded by a ring of papillae.

Remarks: Foliage of this fossil maple morphologically resembles *Vitis* but the epidermal structure places it into *Acer* sect. *Acer* near the modern *A. trautvetteri* Medwedew living in the northern Turkey and the Caucasus (cf. Grimm et al. 2007).

Aesculus Linnaeus

Aesculus hippocastanoides Iljinskaja

Fig. 12a–c

1968 *Aesculus hippocastanoides* Iljinskaja, p. 79, pl. 24, fig. 8, pl. 27, figs. 1–3, pl. 28, figs. 4–6, pl. 29, fig. 8, pl. 36, figs. 2–3

Material: SF.B 12342, 12390, 12391, 12392.

Description: Leaflets short petiolulate, petiolule broadened at point of attachment, 5 mm long; lamina obovate, ca. 50 mm long and 24 mm wide, incomplete at apices, base cuneate, simple dentate, teeth regularly closely spaced, falcate, venation semicraspedodromous, primary vein thick and straight, secondary veins dense, straight, bent near margin, sending minute outer veinlets into teeth, tertiary veins mixed percurrent (sample SF.B 12392). Adaxial cuticle smooth, straight-walled, abaxial cuticle finely papillate, stomata rarely preserved, anomocytic, rounded.

Remarks: The material shows affinities to the North American members of sect. *Pavia* (Mill.) Persoon based on the long petiolulate leaflets and epidermal anatomy. The leaves were probably produced by the same species as the fruit and seed fragments described from the same site by Engelhardt (in Engelhardt and Kinkelin 1908). Similar leaflets were described from the

Pliocene of Willershausen (Straus 1930, as *Aesculus* cf. *pavia* Linnaeus, Knobloch 1998, as *A. velitzelosii* Erw. Knobloch). Some other records of *Aesculus* foliage not preserved with leaf anatomy (Iljinskaja 1968, as *A. hippocastanoides* Iljinskaja, Walther in Mai and Walther 1988, as *A. cf. hippocastanum* Linnaeus, Grimsson et al. 2007, as *Aesculus* sp.) match well in petiolulate leaflets, differing from the modern European *A. hippocastanum* with sessile leaflets.

Meliaceae Jussieu

“*Juglans*” *acuminata* A. Braun

Figs. 12d, e and 19c–f

1845 *Juglans* (? *Carya*) *acuminata* A. Braun, p. 170, nom. nud.

1850 *Juglans acuminata* A. Braun; Unger, p. 468

1994 *Cedrela acuminata* (A. Braun) Iljinskaja, p. 76

Material: SF.B 11664, 11665, 11666, 11667, 11668.

Description: Leaflets shortly petiolulate, petiolule max. 5 mm long, lamina entire-margined, asymmetrically ovate to oblong, up to > 100 mm long, 24–32 (–45) mm wide, apex acuminate, base truncate, rounded to widely cuneate, venation brochidodromous, primary vein thick, slightly curved, secondary veins in more than 13 pairs, secondary veins alternate to sub-opposite, slightly s-shaped, more closely spaced towards apex, slightly curved, looping near margin, single intersecondary veins commonly present, tertiary veins alternate percurrent, quaternary veins regular reticulate. Epidermal anatomy (sample 11668), adaxial cuticle faintly striate, reflecting polygonal outlines of straight-walled ordinary cells 20–25 µm in diameter, anticlinal walls straight, solitary trichome bases simple, rounded, 12 µm in diameter, abaxial cuticle irregularly finely striate, rarely with preserved rounded to elliptic head up to 120 µm long and 70 µm wide, cell outlines not observable, stomata elliptic, anomocytic, all of the same size, 15–20 × 12 µm, stomatal ledges slightly thickened, outer cavity elliptic, boat-shaped, 12–15 µm long, rare simple filamentous trichomes up to 120 µm.

Remarks: This fossil species has been commonly recorded in the European Neogene and is quite characteristic in leaf morphology (e.g. Bůžek 1971). The epidermal structure clearly differs by peltate glandular trichomes from the modern species of *Juglans* including *J. regia* Linnaeus, usually cited as a modern analogue. A typical, broader form of “*Juglans*” *acuminata* from Arjuzanx (Kvaček et al. 2011) showed also peltate glandular trichomes in an unmacerated specimen embedded between glass slides. Morphologically similar but narrower impressions from the Pliocene of Willershausen (Knobloch 1998) were assigned to *Cedrela heliconia* (Unger) Erw. Knobloch, those from the Sarmatian from Bulgaria to *Cedrela attica* (Unger) Palamarev et Petkova (Palamarev et al. 2005).

◀ **Fig. 14** **a** *Viscum miquelii* (Geyler et Kinkel) Czechtz, complete leaf, SF.B 12461, 10 mm. **b** *Viscum miquelii* (Geyler et Kinkel) Czechtz, complete leaf, neolectotype S 082703, 10 mm. **c** *Viscophyllum pliacaenicum* (Engelhardt) Mädl, incomplete leaf, SF.B 12444, 10 mm. **d** *Viscophyllum pliacaenicum* (Engelhardt) Mädl, incomplete leaf, neolectotype V.17170, 10 mm. **e** *Viscophyllum pliacaenicum* (Engelhardt) Mädl, incomplete leaf, SF.B 12445, 10 mm. **f** *Eucommia szaferei* Kvaček, Teodoridis et Denk sp. nov., incomplete leaf, SF.B 12396, 10 mm. **g** *Eucommia szaferei* Kvaček, Teodoridis et Denk sp. nov., fruit, SF.B 12163, 10 mm. **h** *Fraxinus angusta* Hummel, incomplete leaflet, SF.B 12405, 10 mm. **i** *Fraxinus angusta* Hummel, complete leaflet, SF.B 12424, 10 mm. **j** *Ilex geissertii* Kvaček, Teodoridis, Wang Qing, incomplete leaf, SF.B 12780, 10 mm. **k** *Dicotylophyllum* sp. A, incomplete leaf, SF.B 12384, 10 mm. **l** *Dicotylophyllum* sp. B, incomplete leaf, SF.B 12403, 10 mm. **m** *Dicotylophyllum* sp. B, complete leaf, SF.B 12399, 10 mm

The abundant foliage of *J. acuminata* is associated with seeds of the *Toona* type at the early Miocene site Čermný in North Bohemia (Bůžek 1971, p. 102, pl. 24, figs. 20–21, as *Fructus vel semen*). The affinity of the record from Frankfurt/M. to the Meliaceae is clearly demonstrated by the indumentum of the leaf. Foliage of various genera of Meliaceae is morphologically similar (e.g. *Toona* (Endlicher) M. Roemer of Asia and Australia, *Cedrela* P. Browne, *Swietenia* Jacquin of Mexico and Central America) but a lepidote indumentum is rarely present (e.g. in *Aglaiia* Loureiro from the Philippines, Indonesia to Taiwan). Most modern species of *Aglaiia* distributed in East and Southeast Asia (to Australia) have a lepidote foliage and match also in leaf morphology (e.g. *A. lawii* (Wight) C.J. Saldanha from Taiwan, Yunnan and elsewhere in southern Asia). Contrary to the mentioned evergreen representatives of Meliaceae, the studied fossil specimens differ by a papery (obviously deciduous) leaf lamina. In other occurrences of “*Juglans*” *acuminata*, most specimens are isolated leaflets and complete leaves are extremely rare (Heer 1859). We are unable to assign “*Juglans*” *acuminata* to a particular genus of the Meliaceae. Fossil *Cedrela merrillii* (Chaney) P. Brown from the North American Cenozoic differs by the wavy margin of the leaflets and associated seeds as documented by Meyer and Manchester (1997), 131, pl. 54, figs. 1–12).

Malvaceae Jussieu

Hibiscus Linnaeus

Hibiscus sp.

Figs. 12f, g and 18o

? 1965 *Hibiscus splendens* Bajkovskaja in Kryshotofowicz et Bajkovskaja, p. 110, pl. 32, fig. 6, pl. 33, figs. 2–3, pl. 34, fig. 6

Material: SF.B 12252, 12263, 12263/1, 12347, cuticle preparation SF.B 12263.1–2.

Description: Leaves cordate, pentalobate to trilobate, widely coarsely toothed on abmedial margin of side lobes and medial lobe, partly entire, teeth apiculate, cuticles thin, adaxial cuticle showing straight-walled anticlines, cylindrical barrel-shaped

glands divided into four to six segments dispersed on veinlets, stomata anomocytic, broadly elliptic, ledges thinly cutinised, pore short.

Remarks: A few compressions imitate *Vitis* and *Acer* in leaf morphology while leaf anatomy, particularly the indumentum with barrel-shaped polycellular glands clearly indicates Malvales (Kvaček and Wilde 2010). Foliage of some modern species of *Hibiscus* (e.g. *H. mutabilis* Linnaeus) is closely similar to the fossil species from Frankfurt. The previously described *Hibiscus splendens* Bajkovskaja, nom illegit. (non Graham) from the middle Miocene of Ukraine differs in less distinctly toothed margins.

Dombeyopsis Unger

aff. *Dombeyopsis lobata* Unger

Fig. 12h

1850 *Dombeyopsis lobata* Unger, p. 447

Material: SF.B 12194, ? 12220.

Description: One incomplete leaf base, leaf long petiolate, lamina deeply cordate, entire-margined, venation actinodromous, midrib and six lateral basal veins. Another incomplete leaf with shallow cordate base, actinodromous venation, and five basal veins may rather belong to a maple because of a single tooth on the lateral part.

Remarks: The compressions are not accessible for cuticle preparation. They co-occur at the site, with fruit remains of *Craigia bromnii* (as *Ulmus longifolia* Unger in Kräusel 1939, p. 86, pl. 8, fig. 2 and in Kräusel 1940, text-fig. 9b).

Tilia Linnaeus

? *Tilia* sp.

Fig. 12i

Material: SF.B 12271.

Description: Incomplete small leaf without attached petiole, lamina cordate, lobate, broadly elliptic, middle lobe coarsely dentate, venation camptodromous to semicraspedodromous.

Remarks: Besides isolated bracts of *Tilia* (SF.B 12386, 12389, 12429), the associated incomplete leaf compression SF.B 12271 may represent foliage of this plant.

Santalaceae R. Brown (incl. Viscaceae Batsch)

Viscum miquelii (Geyler et Kinkel) Czechtz

Figs. 14a, b and 19a

Material: S082696, S082703, SF.B 12455–12465, V. 17153, V. 17165, V. 17166, V. 26387, V. 26388.

Neolectotype: Specimen no. S082703 (Fig. 14b).

Description: Leaves elliptic, base widely cuneate and narrowing towards stout petiole, apex rounded, margin entire, venation basal acrodromous, five primary veins straight, venation of higher-order ramified.

◀ **Fig. 15** **a** *Cryptomeria rhenana* Kilpper, adaxial cuticle, S117681.1, 50 µm. **b** *Cryptomeria rhenana* Kilpper, adaxial cuticle, S117681.1, 50 µm. **c** *Cryptomeria rhenana* Kilpper, abaxial cuticle, S117681.1, 100 µm. **d** *Picea omoricoides* C.A. Weber, adaxial cuticle, S117942.1, 50 µm. **e** *Picea omoricoides* C.A. Weber, adaxial cuticle, S117942.1, 50 µm. **f** *Picea omoricoides* C.A. Weber, adaxial cuticle, S117942.1, 50 µm. **g** *Sciadopitys tertiaria* Menzel, adaxial cuticle, S118054.1, 50 µm. **h** *Sciadopitys tertiaria* Menzel, adaxial cuticle, S118054.1, 50 µm. **i** *Sequoia abietina* (Brongniart) Erw. Knobloch adaxial cuticle, S118125, 50 µm. **j** *Glyptostrobus europaeus* (Brongniart) Unger adaxial cuticle, S118207.1, 50 µm. **k** *Glyptostrobus europaeus* (Brongniart) Unger adaxial cuticle, S118207.1, 50 µm. **l** *Glyptostrobus europaeus* (Brongniart) Unger adaxial cuticle, S118207.1, 100 µm. **m** *Pseudotsuga kinkelinii* (Mädler) Kvaček, Teodoridis et Denk comb. nov., S082700, 50 µm. **n** *Pseudotsuga kinkelinii* (Mädler) Kvaček, Teodoridis et Denk comb. nov., S082700, 50 µm. **o** *Pseudotsuga kinkelinii* (Mädler) Kvaček, Teodoridis et Denk comb. nov., S082700, 25 µm

Remarks: The epidermal anatomy and relationship of the fossil species have been described and discussed several times (Knobloch and Kvaček 1976; Kovar-Eder and Krainer, 1991; Kvaček et al. 2008).

Viscophyllum pliocaenicum (Engelhardt) Mädler
Figs. 14c–e and 19b

1908 *Potamogeton pliocenicum* Engelhardt in Engelhardt and Kinkelin, p. 225, pl. 27, fig. 25a–n
1939 *Viscophyllum pliocaenicum* (Engelhardt) Mädler, p. 91, pl. 8, figs. 8–9, pl. 11, fig. 5

Material: Original slides S082698, V.17170, V.25389, V.26336, V.26390, new material SF.B 12444, 12445, 12449, 12450.

Neoelectotype: Specimen no. V17170 (fig. 14d).

Description: Leaves linear, up to 60 mm long and up to 5 mm wide, apex rounded, base truncate, margin entire, venation basal acrodromous, three primary veins straight, venation of higher-order ramified.

Remarks: The above listed material corresponds exactly to the partly destroyed type material. A new lectotype is established from the remaining specimens.

Eucommiaceae Engler

Eucommia Oliver

Eucommia szaferi Kvaček, Teodoridis et Denk sp. nov.

Figs. 14f, g and 19g–j

1954 *Eucommia europaea* Mädler sensu Szafer, p. 29, pro parte, pl. 6, figs. 9–14–15 (non 9–13, fruits)
1997 *Eucommia* sp., Hably and Kvaček, p. 37, pl. 16, figs. 84–86
2008 *Eucommia* sp., Kvaček, Teodoridis and Gregor, p. 12, pl. 14, fig. 9–10, pl. 15, figs. 1, 3, pl. 23, figs. 11–13, pl. 24, figs. 3–4

Holotype established here: SF.B 12396 (fig. 14f) and cuticle preparation SF.B 12396.1.

Other type material: SF.B 12160, 12162a, 12394, 12395, 12397?, 12398, 12402, 12473.

Derivatio nominis: In honour of the late Polish palaeobotanist, Prof. Władisław Szafer, Cracow, who firstly recognised foliage of *Eucommia* in the European Neogene.

Description: Leaves simple ovate, long petiolate, blade minutely serrate, venation semicraspedodromous. Adaxial cuticle faintly striate, unspecialised cells polygonal, 13–25 µm in diameter, anticlinal walls straight to slightly curved, abaxial cuticle fragmentary, anticlinal walls of ordinary cells slightly curved to shallow wavy, stomata anomocytic, elliptic, 17 µm long, 10 µm wide, dense mesophyllous fine bodies 10 µm in diameter, dense gutapercha strands on veins.

Remarks: After the discovery of *Eucommia* fruits (Mädler 1939), Szafer (1954) reported a rich fossil record of this exotic plant (fruits, leaves) in the Polish Pliocene flora near Czorsztyn. Similar *Eucommia* leaves accompany the characteristic fruits at several Neogene sites in Europe (see Kvaček et al. 2008). They can be readily discriminated by gutapercha strands in the veins. Leaf impressions matching *Eucommia* in gross morphology have been described from the European Neogene in several cases and probably misinterpreted as they imitate alder foliage (e.g. *Alnus acutidens* Boulay 1890, pl. 6, fig. 9, Thésiers, France). Foliage attributed to *Eucommia* from the Sarmatian of Ukraine (*E. palaeoulmoides* Kryštofowich et Bajkovskaja 1965) differs by its double dentate margin and requires re-examination.

Oleaceae Hoffmannsegg et Link

Fraxinus Linnaeus

Fraxinus angusta Hummel

Figs. 14h–i and 19k–m

1983 *Fraxinus angusta* Hummel, p. 79, pl. 51, figs. 1–4a, pl. 52, figs. 1–5a, pl. 53, figs. 1–6, text-figs. 31.9–20, 32.1–7

1998 *Fraxinus pliocenica* Erw. Knobloch, p. 81, pl. 54, fig. 1, pl. 59, figs. 1–4, pl. 61, figs. 4, 8

Material: SF.B 12404, 12405, 12406, 12407, 12409, 12410, 12411, 12423, 12424, 12425, 12426, 12427, cuticle preparation SF.B 12404.1.

Description: Leaflets sessile or shortly petiolulate, lamina ovate to elliptical, rounded at base, long acuminate at apex, fine serrate, venation semicraspedodromous, primary vein slightly curved, secondaries in more than 10 pairs, exterior tertiary veins terminating at margin. Adaxial cuticle smooth, ordinary cells 25–30 (–50) µm in diameter, anticlines coarsely undulate, solitary trichome bases rounded, with the periphery seen as a double line, rarely a peltate circular gland attached. Abaxial cuticle thin, slightly striate, stomata closely distributed, variable in size, anomocytic, elliptical, 15–30 µm long, 12–20 µm wide, stomatal ledges boat-like, slightly thickened, peltate solitary glands with 8–16-celled shield, 35–50 µm in

◀ **Fig. 16** **a** *Pseudotsuga sclereidea* (Mädler) Kvaček, Teodoridis et Denk comb. nov., S082707, 50 µm. **b** *Taxus* aff. *baccata* Linnaeus, adaxial cuticle, S082870, 50 µm. **c** *Taxus* aff. *baccata* Linnaeus, abaxial cuticle, S082870, 50 µm. **d** *Sassafras* cf. *ferretianum* Massalongo et Scarabelli, adaxial cuticle, SF.B 12157, 50 µm. **e** *Sassafras* cf. *ferretianum* Massalongo et Scarabelli, abaxial cuticle, SF.B 12157, 50 µm. **f** *Magnolia waltheri* Kvaček, Teodoridis et Denk sp. nov., adaxial cuticle, SF.B 12157.1, 50 µm. **g** *Magnolia waltheri* Kvaček, Teodoridis et Denk sp. nov., abaxial cuticle, SF.B 12157.1, 50 µm. **h** *Magnolia waltheri* Kvaček, Teodoridis et Denk sp. nov., adaxial cuticle, SF.B 12169.2, 50 µm. **i** *Magnolia waltheri* Kvaček, Teodoridis et Denk sp. nov., abaxial cuticle, SF.B 12169.2, 50 µm. **j** *Magnolia liblarensis* (Kräusel et Weyland) Kvaček, adaxial cuticle, SF.B 12438.1, 50 µm. **k** *Magnolia liblarensis* (Kräusel et Weyland) Kvaček, abaxial cuticle, SF.B 12438.1, 50 µm. **l** *Magnolia liblarensis* (Kräusel et Weyland) Kvaček, abaxial cuticle, (phase contrast) B 12438.1, 50 µm. **m** *Buxus pliocaenica* Saporta, adaxial cuticle, S 082705, 50 µm. **n** *Buxus pliocaenica* Saporta, abaxial cuticle, S 082705, 50 µm. **o** *Pachysandra europaea* Kvaček, Teodoridis et Denk sp. nov., adaxial cuticle, SF.B 12393, 50 µm

diameter, stalk simple, 12 µm across, trichome bases small rounded, simple.

Remarks: Both leaf morphology and epidermal anatomy indicate the affinity to *Fraxinus*. The epidermal structure corresponds to the description and illustration of *Fraxinus angusta* Hummel (1983) so far known only from the Pliocene site Ruzów, Poland. Morphologically similar foliage was described from the Pliocene flora of Willershausen (Knobloch 1998) including associated fruits and complete compound leaves. According to Hummel (1983), the epidermal structure of *Fraxinus angusta* is most similar to that of the modern *F. excelsior* Linnaeus native to Europe to Caucasus. Fruits of *Fraxinus* have also been recorded in the carpoflora of Frankfurt (Mädler 1939).

Aquifoliaceae Berchtold et J. Presl

Ilex Linnaeus

Ilex geissertii Kvaček, Teodoridis, Wang Qing

Figs. 14j and 19n

1939 *Ilex aquifolium* Linnaeus *fossilis* Engelhardt; Mädler, p. 110, pl. 8, fig. 35, pl. 13, fig. 3

2008 *Ilex aquifolium* Linnaeus *fossilis* Engelhardt; Kvaček, Teodoridis and Gregor, p. 28, pl. 8, figs. 10–13, pl. 20, figs. 3–5

2009 *Ilex geissertii* Kvaček, Teodoridis, Wang Qing, p. 199, pls. 1–4, 8, figs. 1–6

Material: Original material of Mädler (1939) V. 17175, S082690, S082699; new specimens SF.B 12374, 12365, 12372, 12373, 12375, 12377, 12381, 12378, 12476, 12383, 12382, 12371, 12364, 12363, 12361, 12362, 12370, 12369, 12368, 12367, 12366.

Description: See Kvaček et al. (2009).

Remarks: For detailed description and comments, see Kvaček et al. (2009).

Angiospermae incertae familiae

Dicotylophyllum Saporta

The leaf remains described below cannot be assigned to particular families and genera in most cases. Remarks are only provided in cases where closer similarities to some taxa are observed. Cuticle preparations are available in rare cases, when leaf specimens were accessible to remove cuticle samples.

Dicotylophyllum sp. A

Fig. 14k

Material: SF.B 12384.

Description: Leaf ovate to lanceolate, entire-margined, base decurrent, lamina grading into a short stout petiole, base narrow cuneate, apex missing, venation camptodromous.

Remarks: This leaf remain conforms with the overall leaf morphology of *Nyssa*. Mädler (1939) reported stone fruits of *Nyssa* in the Pliocene flora of Frankfurt.

Dicotylophyllum sp. B

Fig. 14l–m

Material: SF.B 12399, 12401, 12403, 12436, 12700.

Description: Leaf, petiolate, petiole 4 to > 10 mm, lamina elliptic, > 40 and 60 mm long, entire margined but with minute glandular teeth, secondary venation brochidodromous, with additional loops, intersecondary veins present, departing from primary vein at lower angles than secondary veins.

Remarks: Similar leaves are found in the Japanese extant species *Styrax japonicus* Siebold et Zuccarini. Mädler (1939) reported abundant seeds of *Styrax obovatum* (Weber) Mädler from the same site. According to Mädler, the fossil seeds are more similar to the Japanese *S. japonicus* than to the Mediterranean *S. officinalis* Linnaeus. The fossil differs from *S. japonicus* in the longer apical extension of the seed.

Dicotylophyllum sp. C

Fig. 13a

Material: B 12433.

Description: Leaf apex broadly elliptic to rounded, margin sub-entire, with widely scattered minute teeth.

Remarks: The fragment may represent the apex of a leaf of *Dicotylophyllum* sp. B.

Dicotylophyllum sp. D.

◀ **Fig. 17** **a** *Pachysandra europaea* Kvaček, Teodoridis et Denk sp. nov., abaxial cuticle, SF.B 12393, 50 µm. **b** *Gleditsia pliocaenica* Kvaček, Teodoridis et Denk sp. nov., abaxial cuticle, SF.B 12414.1 50 µm. **c** ? *Prunus* sp., adaxial cuticle, SF.B 12387.2, 50 µm. **d** ? *Prunus* sp., abaxial cuticle with trichome bases, SF.B 12387.2, 50 µm. **e** ? *Prunus* sp., abaxial cuticle, SF.B 12387.1, 50 µm. **f** *Castanea* sp., abaxial cuticle, SF.B 11836, 50 µm. **g** *Castanea* sp., trichome base, SF.B 11836, 50 µm. **h** *Quercus roburoides* Gaudin sensu Erw. Knobloch, abaxial cuticle, SF.B 11805, 50 µm. **i** *Quercus pseudocastanea* Göppert sensu Walther et Zastawniak abaxial cuticle, SF.B 11786, 50 µm. **j** *Quercus praecastaneifolia* Erw. Knobloch abaxial cuticle, SF.B sn 11, 50 µm. **k** *Quercus* sp. abaxial cuticle, SF.B 11643, 50 µm. **l** *Betula similis* (Göppert) Zastawniak et Walther adaxial cuticle, SF.B 11806, 50 µm. **m** *Betula similis* (Göppert) Zastawniak et Walther abaxial cuticle, SF.B 11806, 50 µm. **n** *Trichosanthes* sp., abaxial cuticle with trichomes, SF.B 12191.1, 50 µm

Figs. 13b, 19o and 20a

Material: SF.B 12440, cuticle preparation SF.B 12440.1.

Description: Leaf lanceolate, margin sub-entire, sessile, venation brochidodromous with additional loops from which fine veins enter minute teeth, abaxial cuticle finely papillate, papillae 5 µm across, stellate striation around stomata, stomata rounded elliptic, their maximum size 35 × 20 µm, ledges thin and broad, pore spindle-shaped, slightly thickened, a single observation of a peltate trichome, ca. 50 µm across, with simple thick base.

Remarks: By its leaf shape, this specimen resembles *Salix*; the venation is similar to *Pterocarya* or *Cyclocarya*. At this point, the botanical affinities remain uncertain.

Dicotylophyllum sp. E

Fig. 13c

Material: SF.B 12434.

Description: Leaf narrow oblanceolate, margin sub-entire, with solitary widely spaced minute teeth, base narrow cuneate and decurrent into a short stout petiole.

Dicotylophyllum sp. F

Fig. 13d

Material: SF.B 12435.

Description: Leaf elliptic, incomplete, long petiolate, margin entire, venation eucamptodromous.

Remarks: Similar to *Diospyros* Linnaeus.

Dicotylophyllum sp. G

Fig. 13e

Material: SF.B 12441.

Description: Leaf or leaflet, lamina elliptic, base rounded asymmetric, apex not preserved, margin sub-entire, with solitary distinct teeth in the lower part of the lamina and indistinct teeth higher up on one side of lamina, other side of lamina entire.

Remarks: This leaf remain might be a leaflet of a compound leaf.

Dicotylophyllum sp. H

Figs. 13f and 20c

Material: SF.B 12442, cuticle preparation SF.B 12442.1.

Description: Leaf, lamina broad entire-margined rounded base, sessile (?), margin entire, venation brochidodromous. Cuticle thin, smooth, fine striations on veins, anticlinal walls straight, unspecialised cells 12–15 µm in diameter, stomata probably on either leaf side, anomocytic (?), broadly elliptic, 15–37 long, 12–30 µm wide, size variable, outer stomatal ledges only slightly thickened, reaching to poles, surrounding boat-shaped aperture up to 25 µm long and 12 µm wide, single thin-walled trichome bases 5–12 µm across, densely dispersed on veins.

Dicotylophyllum sp. I

Fig. 13g

Material: SF.B 12433.

Description: Fragment of leaf, petiolate, base rounded acute, lamina narrow elliptic, margin entire, venation brochidodromous.

Dicotylophyllum sp. J

Figs. 13h and 20d–f

Material: SF.B 12431, cuticle preparation SF.B 12431.1.

Description: Leaf fragment, lamina elliptic, secondary venation brochidodromous, loops widely spaced, intersecondary veins present, margin covered with short hairs, cuticles extremely thin, adaxial cells with coarsely wavy anticlines, up to 50 µm in diameter, narrow polycellular trichome-like fringes on margin, abaxial cuticle smooth, fine papillate, anticlinal walls of unspecialised cells undulate, stomata probably anomocytic, broadly elliptic, 20–22 µm long, 15 µm wide, ledges wide and thin, butterfly-like, surrounding very narrow pore, rare mesophyllous bodies present, 38–56 µm in diameter, cracked, solitary polycellular bases ca. 50 µm in diameter, thin.

Remarks: Similar to some narrow-leaved modern species of *Lonicera* (e.g. *L. maximowiczii* (Ruprecht) Regel, *L. angustifolia* Wallich ex DC.) by the ciliate margin. All the so far published fossil foliage assigned to *Lonicera*, mostly from the European late Miocene and Pliocene, e.g. *L. liphayana* Andreánszky (Andreánszky 1959; Palamarev and Kitanov 1988), *Lonicera etrusca* Santi (Stojanoff and Stefanoff 1929, p. 93, fig. 11, pl. 12, fig. 22, text-fig. 23), cf. *L. etrusca* Santi ? (Pop 1936, p. 98, 168, pl. 21, fig. 2), *L. nigra* Linnaeus (Stojanoff and Stefanoff 1929, 93, fig. 10, pl. 12, fig.

◀ **Fig. 18** **a** *Salix* cf. *lavateri* A. Braun sensu Hantke, adaxial cuticle, SF.B 11623.1, 50 µm. **b** *Salix* cf. *lavateri* A. Braun sensu Hantke, adaxial cuticle, SF.B 11623.1, 50 µm. **c** *Salix* cf. *lavateri* A. Braun sensu Hantke, abaxial cuticle, SF.B 11623.1, 50 µm. **d** *Populus balsamoides* Göppert, abaxial cuticle, SF.B 11670.1, 50 µm. **e** *Populus balsamoides* Göppert, abaxial cuticle, SF.B 11670.1, 50 µm. **f** *Acer dombeyopsis* Kvaček, Teodoridis et Denk sp. nov., adaxial cuticle, SF.B 12211.1, 50 µm. **g** *Acer dombeyopsis* Kvaček, Teodoridis et Denk sp. nov., abaxial cuticle, SF.B 12211.1, 50 µm. **h** *Acer subcampestre* Göppert, adaxial cuticle, SF.B 12324.1, 50 µm. **i** *Acer subcampestre* Göppert, abaxial cuticle, SF.B 12324.1, 50 µm. **j** *Acer viburnoides* Kvaček, Teodoridis et Denk sp. nov., abaxial and adaxial cuticle, SF.B 12210, 50 µm. **k** *Acer* aff. *platanoides* Linnaeus, abaxial cuticle, SF.B 12219.1, 50 µm. **l** *Acer* aff. *platanoides* Linnaeus, abaxial cuticle, SF.B 12324.1, 50 µm. **m** *Acer vitiforme* Kvaček, Teodoridis et Denk sp. nov., adaxial cuticle, SF.B 12319.1, 50 µm. **n** *Acer vitiforme* Kvaček, Teodoridis et Denk sp. nov., abaxial cuticle, SF.B 12319.1. **o** *Hibiscus* sp., abaxial cuticle with trichomes, SF.B 12191.1, 50 µm

23, text-fig. 23), *L.* cf. *xylosteum* Linnaeus (Stefanoff and Jordanoff 1934, p. 36, pl. 3, fig. 21, pl. 8, figs. 19–20), *Lonicera* sp. A, B (Kryštofovich and Baikovskaja 1965, p. 122, pl. 37, fig. 4, pl. 39, fig. 9) differ in the broader form (see also Němejč 1975, text-fig. 57.11). The leaf impressions from the middle Miocene of Island (see Grímsson et al. 2007; Denk et al. 2005, p. 410, figs. 203–206, as *Dicotylophyllum* sp. 2 (“*Lonicera*”); Grímsson et al. 2007, p. 21 as *Lonicera* sp.; Grímsson et al. 2007, pl. 9, figs. 5–6, as *Dicotylophyllum* sp. 1 (“*Lonicera*” sp.) are similar in venation pattern but are broader and do not show the ciliate margin. The ciliate margin alone is not genus diagnostic because such ciliate leaves are produced by more dicots, e.g. *Diervilla lonicera* Miller (eastern North America) and others (e.g. *Rhododendron* Linnaeus).

Dicotylophyllum sp. K
Figs. 13i

Material: SF.B 12430.

Description: Leaf, petiolate, lamina fragmentary, only basal part preserved, margin entire, secondary veins densely spaced, brochidodromous.

Remarks: Leaf may be similar to Maloideae C. Weber.

Dicotylophyllum sp. L
Figs. 13j and 20b

Material: SF.B 12437, cuticle preparation SF. B 12437.1.

Description: Leaf, lamina elliptic, base cuneate, apex probably acuminate, margin entire, secondary venation eucamptodromous to brochidodromous, secondary veins branching once or twice. Cuticles of both adaxial and abaxial sides extremely thin, adaxial cuticle showing polygonal straight-walled cells, abaxial cuticle smooth, ordinary cells with wavy anticlines, stomata anomocytic, broadly elliptic, 25 µm long, 15–18 µm wide, ledges thin, double, pore broadly elliptic, trichome bases simple rounded, 10–12 µm in diameter, dense near veins, surrounded by a rosette-like ring of

quadrangular straight-walled isodiametric subsidiary cells, occasionally peltate glands and solitary simple trichomes preserved.

Remarks: This single leaf compression resembles in leaf morphology deciduous species of *Rhododendron*. Similar stomata and trichome bases were found in the entire-margined leaf fragment identified as ? “*Diospyros*” *brachysepala* Heer from the Pliocene of Gércé, Hungary (Hably and Kvaček 1997).

Dicotylophyllum sp. M
Fig. 13k

Material: SF.B 12156.

Description: Leaf base, long petiolate, narrow elliptic, not decurrent, margin entire, venation eucamptodromous.

Remarks: This foliage is similar to *Laurophyllum* but no lens-shaped oil cells were observed. It is also similar to *Magnolia* but the leaf epidermal features are insufficient to securely place it within this genus.

Dicotylophyllum sp. N
Fig. 13l

Material: SF.B 12176.

Description: Leaf apex acute, margin finely simple toothed, venation semicraspedodromous.

Dicotylophyllum sp. O
Figs. 13m and 20g, h

Material: SF.B 12177, 12178, 12179, 12180, 12181, 12182, cuticle preparation SF. B 12180.1.

Description: Leaves petiolate, ovate–elliptic, apex cuneate, base rounded, asymmetric, margin regularly sharply spinulose simple serrate, venation semicraspedodromous. SF. B 12180.1: Cuticles extremely thin, unspecialised cells with straight or slightly curved anticlines, stomata ? anomocytic, elliptic, 10–12 µm long, 7–10 µm wide, pore narrow spindle-shaped, reaching to poles, ledges not thickened; peltate glands on veins with entire-margined head, 120 µm in diameter, on simple rounded stalk, 15 µm in diameter.

Remarks: In marginal dentition, these leaves are similar to *Clethra* and Rosaceae. According to the leaf gross morphology (long petiolate leaves with spinulose margin and semicraspedodromous venation patterns), the fossil species resembles the Rosaceae subfamily Maloideae C. Weber, namely *Pyrus ussuriensis* Maximowicz native to Korea, Japan and the Ussuri River area of the Russian Far East, and allied Chinese species (see Rehder 1915). These species typically have leaves with long spinulose–serrate margin. However, the peltate glands found on the abaxial leaf side of one of the specimens (SF.B 12180) make the affinity to the Rosaceae improbable. Comparable leaves were assigned to *Clethra* Linnaeus from the Romanian late Miocene site Chiuzbaia (Givulescu 1990). The

Fig. 19 **a** *Viscum miquelii* (Geyler et Kinkelien) Czeccott, leaf cuticle, S 082696.1, 50 μ m. **b** *Viscophyllum pliocaenicum* (Engelhardt) Madler, leaf cuticle S 082697.1, 50 μ m. **c** “*Juglans*” *acuminata* A. Braun, adaxial cuticle, SF.B 11668.2, 50 μ m. **d** “*Juglans*” *acuminata* A. Braun, abaxial cuticle, SF.B 11668.2, 50 μ m. **e** “*Juglans*” *acuminata* A. Braun, abaxial cuticle, SF.B 11668.2, 50 μ m. **f** “*Juglans*” *acuminata* A. Braun, abaxial cuticle with trichome bases, SF.B 11668.2, 50 μ m. **g** *Eucommia szaferei* Kvaek, Teodoridis et Denk sp. nov., adaxial cuticle, SF.B 12396.1, 50 μ m. **h** *Eucommia szaferei* Kvaek, Teodoridis et Denk sp. nov., adaxial cuticle with gutapercha strands, SF.B 12396.1, 50 μ m. **i** *Eucommia szaferei* Kvaek, Teodoridis et Denk sp. nov., abaxial cuticle, SF.B 12396.1, 50 μ m. **j** *Eucommia szaferei* Kvaek, Teodoridis et Denk sp. nov., mesophyllous bodies, SF.B 12396.1, 50 μ m. **k** *Fraxinus angusta* Hummel, adaxial cuticle, SF.B 12404.1, 50 μ m. **l** *Fraxinus angusta* Hummel, abaxial cuticle, SF.B 12404.1, 50 μ m. **m** *Fraxinus angusta* Hummel, abaxial cuticle with peltate trichomes, SF.B 12404.1, 50 μ m. **n** *Ilex geissertii* Kvaek, Teodoridis, Wang Qing, abaxial cuticle, SF.B 12219.1, 50 μ m. **o** *Dicotylophyllum* sp. D, adaxial cuticle, SF.B 12440.1, 50 μ m

Fig. 20 **a** *Dicotylophyllum* sp. D, abaxial cuticle, SF.B 12440.1, 50 μ m. **b** *Dicotylophyllum* sp. L, abaxial cuticle, SF.B 12437.1, 50 μ m. **c** *Dicotylophyllum* sp. H, abaxial cuticle, SF.B 12442.1, 50 μ m. **d** *Dicotylophyllum* sp. J, adaxial cuticle, SF.B 12431.1, 50 μ m. **e** *Dicotylophyllum* sp. J, abaxial cuticle, SF.B 12431.1, 50 μ m. **f** *Dicotylophyllum* sp. J, abaxial cuticle with mesophyll bodies, SF.B

epidermal anatomy, namely the presence of peltate glandular trichomes, rules out such a systematic interpretation, because the pubescence in *Clethra* differs in stellate, tufted trichomes. This plant was also recovered at the Pliocene site of Auenheim (Kvaek et al. 2008, as *Carya* sp., pro parte, pl. 2, figs. 9, 1).

Discussion

Age of the flora of Frankfurt/M.

The Pliocene flora of Frankfurt/M. was discovered in 1884 and numerous plant fossils were collected after 1885, when

12431.1, 50 μ m. **g** *Dicotylophyllum* sp. O, abaxial cuticle with peltate trichome, SF. B 12180.1, 50 μ m. **h** *Dicotylophyllum* sp. O, abaxial cuticle, SF. B 12180.1, 50 μ m. **i** *Acer integerrimum* (Viviani) Massalongo, adaxial cuticle, SF.B 12243.1, 50 μ m. **j** *Acer integerrimum* (Viviani) Massalongo, abaxial cuticle, SF.B 12243.1, 50 μ m

Table 1 Genera recorded from the Pliocene flora of Frankfurt/M. and their modern biogeographic relationships

Fossil taxon (genus level) [no. species]	wEUR	EA	eNA	wNA
<i>Ginkgo</i>	0	1	0	0
<i>Calocedrus</i>	0	1	0	1
<i>Cryptomeria</i>	0	1	0	0
<i>Glyptostrobus</i>	0	1	0	0
<i>Sequoia</i>	0	0	0	1
<i>Taxodium</i>	0	0	1	1
<i>Abies</i>	1	1	1	1
<i>Picea</i>	1	1	1	1
<i>Pinus</i>	1	1	1	1
<i>Pseudotsuga</i> [2]	0	1	0	1
<i>Tsuga</i>	0	1	1	1
<i>Sciadopitys</i>	0	1	0	0
<i>Cephalotaxus</i>	0	1	0	0
<i>Taxus</i>	1	1	1	1
<i>Torreya</i>	0	1	1	1
<i>Magnolia</i> [2]	0	1	1	0
<i>Sassafras</i>	0	1	1	0
<i>Smilax</i>	1	1	1	1
<i>Buxus</i>	1	1	1	1
<i>Pachysandra</i>	0	1	1	0
<i>Liquidambar</i>	1	1	1	0
<i>Parrotia</i>	1	0	0	0
<i>Cercidiphyllum</i>	0	1	0	0
<i>Gleditsia</i>	1	1	1	0
<i>Podocarpium</i> †	1	1	0	0
<i>Crataegus</i>	1	1	1	1
<i>Malus</i>	1	1	1	1
<i>Prunus</i>	1	1	1	1
<i>Rosa</i>	1	1	1	1
<i>Sorbus</i>	1	1	1	1
<i>Spiraea</i>	1	1	1	1
<i>Ulmus</i> [2]	1	1	1	1
<i>Zelkova</i>	1	1	0	0
<i>Fagus</i>	1	1	1	0
<i>Castanea</i>	1	1	1	0
<i>Quercus</i> [5]	1	1	1	1
<i>Carya</i>	0	1	1	0
<i>Pterocarya</i>	1	1	0	0
<i>Alnus</i>	1	1	1	1
<i>Betula</i>	1	1	1	1
<i>Carpinus</i> [2]	1	1	1	0
<i>Corylus</i>	1	1	1	1
<i>Trichosanthes</i>	0	1	0	0
<i>Salix</i>	1	1	1	1
<i>Populus</i> [4]	1	1	1	1
<i>Celtis</i>	1	1	1	1
<i>Acer</i> [7]	1	1	1	1
<i>Aesculus</i>	1	1	1	1
<i>Meliaceae-Cedrela</i> †	1	0	0	0
<i>Hibiscus</i>	1	1	1	1
<i>Dombeyopsis</i> †	1	0	0	0
<i>Tilia</i>	1	1	1	0
<i>Viscum</i>	1	1	0	0
<i>Eucommia</i>	0	1	0	0
<i>Fraxinus</i>	1	1	1	1
<i>Ilex</i>	1	1	1	1
Total	38	51	38	31

wEUR = western Eurasia, EA = East Asia, eNA = eastern North America, wNA = western North America, † = extinct genus, 1 = present, 0 = absent

a sandy clay lens had become exposed during the construction of the clearing basin of the sewage treatment plant in Frankfurt/Niederrad. The depositional setting of the flora makes a closer age determination difficult, and various authors have suggested a late Miocene, early and late Pliocene, or even Quaternary age for the plant assemblage of Frankfurt/M (cf. Mädlar 1939). The general regional lithology comprises sand and gravel on top of clays or surrounding clay lenses and lignites (Martini et al. 2011). Zagwijn (1960) established a palyno-stratigraphic framework for the late Miocene to early Pliocene in the Netherlands and made a clear distinction between the early Pliocene Brunssumian and the late Pliocene Reuverian. Previously, Reid and Reid (1915) had considered the carpofloras of Reuver and Brunssum coeval. Zagwijn (1960) listed a number of pollen taxa that he considered typical of the Brunssumian and Reuverian stages. The Brunssumian was characterised by high values of *Sequoia*-type pollen and the presence of *Rhus*, *Symplocos*, *Tricolporopollenites* (*Tricolporites*) *megaexactus*, *Edmundipollis edmundi* (*Tricolporites edmundi*), Sapotaceae and Engelhardioideae among others. Other elements, found also in the Frankfurt flora, were common throughout the Pliocene (*Pterocarya*, *Carya*, *Eucommia*, *Aesculus*, *Liquidambar*, *Castanea*; Zagwijn 1960). Kemna and Westerhoff (2007) objected that the *Sequoia*-type pollen peak found by Zagwijn was not a reliable feature to identify the Brunssumian stage but acknowledged that the presence of *Symplocos* and *Edmundipollis edmundi* were more diagnostic of the first half of the Pliocene. According to Stuchlik et al. (2014), the pollen taxon *Edmundipollis edmundi* has closest botanical affinities with the extant genus *Diplopanax* (Cornales, Nyssaceae). Both *Symplocos* and *Diplopanax* are absent from the leaf and carpological record of Frankfurt (Supplementary material File 1).

Mohr (1986) investigated a 2.5-m pollen profile from Willershausen und based on the rare occurrence of *Symplocos*, and the absence of other “older” elements such as Sapotaceae, Engelhardioideae suggested a Reuverian age for the flora of Willershausen. This age was accepted by Knobloch (1998). Mai (1995), based on the presence of warmth-loving relicts, distinguished a “Florenkomplex Brunssum” and a “Florenkomplex Reuver”. While placing Frankfurt/M and the “main fossiliferous horizon” of Auenheim (Alsace) in the Floren-komplex Brunssum, Mai (1995) considered the floras of Willershausen and Berga to be of Reuverian age.

Based on the work by Geissert (1972) and Geissert et al. (1990), Kvaček et al. (2008), fig. 2) correlated the Pliocene leaf flora of Auenheim (Alsace, France) with the “Villafranchian” strata of Geissert (1972) and suggested a late Pliocene age (Reuverian). The leaf flora of Frankfurt/M is virtually identical with the one from

Table 2 Selected climate parameters for relict taxa in the Pliocene flora of Frankfurt

Taxon	Distribution	MAT _{min}	MAT _{max}	MTCM _{min}	MTCM _{max}
<i>Cryptomeria japonica</i>	EA	5.4	21	−3.5	14.2
<i>Cunninghamia lanceolata</i>	EA	2	24.7	−7.2	19.8
<i>Glyptostrobus pensilis</i>	EA	10.6	23	−0.2	15.2
<i>Calocedrus macrolepis</i>	EA	14.3	24.3	4	18.7
<i>Calocedrus decurrens</i>	NA	3.7	19.4	−5.4	8.0
<i>Cephalotaxus fortunei</i>	EA	2.2	23	−7	17.7
<i>Cephalotaxus lanceolata</i>	EA	2.2	18.5	−7	10.5
<i>Cephalotaxus latifolia</i>	EA	9	21.2	0.6	12.8
<i>Cephalotaxus mannii</i>	EA	13.1	24.8	5.4	20.1
<i>Cephalotaxus oliveri</i>	EA	9.3	21.4	−1.7	14.2
<i>Cephalotaxus sinensis</i>	EA	2.6	24.7	−7	19.8
<i>Torreya fargesii</i>	EA	7.3	16.2	−2.5	6.2
<i>Torreya</i> f. var. <i>yunnanensis</i>	EA	6.1	14.3	−1.5	7.6
<i>Torreya grandis</i>	EA	12.7	18.2	0.5	9
<i>Torreya jackii</i>	EA	15.0	17.0	3.5	7.2
<i>Torreya californica</i>	NA	8.0	16.0	0.0	9.0
<i>Taxodium distichum</i>	NA	12.6	24.1	−1.4	19.3
<i>Taxodium mucronatum</i>	NA	13.9	26.1	8.9	24.0
<i>Aesculus assamica</i>	EA	15.1	22.2	5.0	15.1
<i>Aesculus californica</i>	NA	8.6	17.0	1.7	9.2
<i>Aesculus chinensis</i>	EA	3.5	16.9	−6.5	5.5
<i>Aesculus glabra</i>	NA	8.0	24.3	−9.1	10.2
<i>Aesculus octandra</i>	NA	8.0	15.5	−3.8	5.1
<i>Aesculus parviflora</i>	NA	15.4	19.2	4.0	10.1
<i>Aesculus pavia</i>	NA	11.9	21.9	−0.8	15.4
<i>Aesculus sylvatica</i>	EA	12.8	17.4	1.7	7.4
<i>Liquidambar formosana</i>	EA	2.2	24.8	−6.6	20.1
<i>Liquidambar styraciflua</i>	NA	9.3	25.3	−3.6	23.8
<i>Nyssa aquatica</i>	NA	12.0	20.9	−2.4	13.0
<i>Nyssa javanica</i>	EA	8.6	24.0	1.3	19.1
<i>Nyssa leptophylla</i>	EA	15.8	15.8	4.6	4.6
<i>Nyssa ogeche</i>	NA	18.3	20.5	8.9	13.5
<i>Nyssa sinensis</i>	EA	10.6	22.7	−0.2	15.1
<i>Nyssa sylvatica</i>	NA	4.5	23.0	−10.4	18.9
<i>Quercus aliena</i>	EA	2.2	21.0	−15.9	15.1
<i>Quercus aliena</i> v. <i>acutiserrata</i>	EA	5.4	21.0	−13.5	15.1
<i>Quercus fabri</i>	EA	2.6	21.3	−7.0	15.2
<i>Quercus griffithii</i>	EA	5.4	20.5	−2.1	15.1
<i>Sassafras albidum</i>	NA	5.6	22.0	−8.7	15.5
<i>Sassafras tzumu</i>	EA	9.3	22.8	−3.3	14.7

Climate data from Thompson et al. (1999a, 1999b, 2000) and Fang et al. (2011)

MAT = mean annual temperature in C°, MTCM = mean temperature of the coldest month in C°, EA = East Asia, NA = North America

Auenheim (Kvaček et al. 2008 and present study). Therefore, we tentatively suggest a Reuverian age for this leaf flora. Palynofloras from drill cores in the surroundings of Frankfurt/M. and Hanau also suggested a late Pliocene age (Martini et al. 2011).

Comparison of the leaf and carpofloras of Frankfurt

Mädler (1939) described 98 taxa based on fruits and seeds for the Pliocene flora of Frankfurt. Eight species were described as new species (Supplementary material

Fig. 21 Possible climate analogues for the Pliocene of Frankfurt. **a** Walter-climate diagram. Lugano in southern Switzerland has a typical temperate climate, Cf climate according to the Köppen–Geiger climate classification. There is no period during the year where rainfall is a limiting factor; summer months are characterised by highest temperatures and precipitation. **b** Walter-climate diagram. Santander in northern Spain has a sub-Mediterranean climate. Rainfall is limited during the summer months but there is no arid period during the summer as in Mediterranean climates. **c** Climate variables for Lugano indicating, among others, the mean temperature of the coldest month. All figures from Lieth et al. (1999)

Recorded Period: P (1861–1993), T (1951–1993)

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Mean daily temperature [°C]	2.6	4.0	7.6	11.2	15.2	18.8	21.5	21.0	17.4	12.4	7.3	3.7
Mean daily temp., min [°C]	0.0	-1.2	4.9	9.3	11.5	17.0	18.7	18.6	14.0	8.7	5.2	1.8
Mean daily temp., max [°C]	4.7	7.1	10.5	13.4	18.1	21.3	23.8	29.8	20.5	14.0	9.1	10.0
Mean precipitation [mm]	65.7	65.2	114.7	152.2	192.9	183.8	162.9	180.2	175.0	183.9	132.3	78.5
Minimum precipitation [mm]	0.0	0.0	0.0	0.0	8.0	29.0	14.0	6.0	1.0	0.0	1.0	0.0
Maximum precipitation [mm]	285.0	391.0	355.0	512.0	519.0	444.0	387.0	575.0	592.0	797.0	530.0	352.0

File 1). In general, there is a remarkable overlap between taxa found in the leaf and the carpological record (Table 3). Differences between the two records are mainly due to the lack of herbaceous species in the leaf fossil record. Of these, about 10 are strictly aquatic species, while most of the others can thrive in different habitats including wet meadows, riparian sites, forest undergrowth, etc. (Supplementary material File 1). One exception may be the genus *Scleranthus*, which is more common on dry sites and as pioneer in open places (Oberdorfer 1979).

In addition, a number of woody taxa are absent from the leaf record as well. These include Engelhardioideae,

Liriodendron, *Corylopsis*, *Meliosma*, *Nyssa*, *Stuartia*, *Styrax* and others (Supplementary material File 1) and the woody lianas *Vitis* (two species) and *Parthenocissus*. A few taxa (*Populus*, *Quercus*) are much more diverse in the leaf fossil record.

Modern distribution, vegetation signals and climatic ranges of relict taxa in the Pliocene flora of Frankfurt/M

Many elements in the flora of Frankfurt/M. have a relictual extant distribution range. Among the gymnosperms, *Ginkgo*, *Calocedrus*, *Cryptomeria*, *Glyptostrobus*, *Sequoia*, *Taxodium*, *Sciadopitys*, *Cephalotaxus* and

Table 3 Comparison of carpofloras and leaf florae from the Pliocene of Frankfurt

Seeds and fruits recorded in Mädlar (1939)	
Gymnosperms	
25 spp.	1 new species
13 genera	8 also in leaf record
Angiosperms	
78 spp.	8 new species
50 genera	19 also in leaf record
	31 absent from leaf record
Of these:	17 herbs or aquatic herbs
	11 trees or shrubs
	2 woody vines
	1 fabaceous fruit

Torreya have highly relictual extant distributions either disjunct between North America and East Asia or confined to one of them (Table 1). The same is true for many angiosperm taxa such as *Sassafras*, *Liquidambar*, *Cercidiphyllum*, *Eucommia* and *Trichosanthes*.

Besides, several relict areas in western Eurasia harbour many of the plants recorded from Frankfurt. For example, in the Euxinian–Hyrcanian region (northern Turkey, Transcaucasia, to northern Iran), a great number of western Eurasian relict taxa are found (*Buxus*, *Celtis*, *Gleditsia*, *Ilex*, *Parrotia*, *Pterocarya*, *Zelkova*). Remarkably, all the genera reported from Frankfurt are growing in the Botanical Garden of Batumi (Georgia; Sharadze 1987). Trees such as *Cryptomeria*, *Cunninghamia* and *Eucommia* further have naturalised in the hinterland of Batumi (T. Denk, personal observation). A few relict species are confined to small areas in the East Mediterranean region (*Liquidambar orientalis*). Kvaček et al. (2008) noted that most plants from the late Pliocene flora of Auenheim (Alsace) belong to

mesophytic representatives of mixed coniferous and broad-leaved deciduous forests. The same is true for the Pliocene flora of Frankfurt. Overall, the Pliocene flora of Frankfurt can be viewed as an impoverished northern hemispheric Neogene forest flora with numerous exotic elements.

Palaeoenvironmental signals based on the IPR vegetation analysis (e.g. Kovar-Eder et al. 2008; Teodoridis et al. 2011) and CLAMP suggest a transitional vegetation (ecotone) between broad-leaved deciduous forest and mixed mesophytic forest thriving under the following (palaeo)climatic conditions, i.e. mean annual temperature (MAT), 10.6 °C; warmest month mean temperature (WMMT), 22.3 °C; coldest month mean temperature (CMMT), –0.1 °C; precipitation of the three wettest consecutive months (3-WET), 764.1 mm; and 3-DRY, 166.8 mm. The reconstructed climate parameters correspond to those of the coeval floras of Auenheim (Teodoridis et al. 2009) and Berga (Teodoridis and Kvaček 2015). The specific structure of the zonal woody key components of Frankfurt/M. i.e. broad-leaved deciduous (BLD)—75.7%, broad-leaved evergreen (BLE)—15.6%, sclerophyllous + legume-like (SCL + LEG)—9.1%, dry herb (DRY HERB)—4% and mesophyllous herb (MESO HERB)—3.3%, shows closest similarity based on the structure of zonal components to modern plant assemblages (mapping units) of “G56 – Balkanic-Rhodopean Oriental hornbeam-hop-hornbeam forests (*Ostrya carpinifolia*, *Carpinus orientalis*), partly with *Haberlea rhodopensis*” from Bulgaria and Greece and “F75 – Armorican (sessile oak-) beech forests (*Fagus sylvatica*, *Quercus petraea*) with *Ilex aquifolium*, *Taxus baccata*, *Ruscus aculeatus*, *Blechnum spicant*” from France and Great Britain (Bohn et al. 2004; see Supplementary material File 4). The climates under which these modern plant assemblages thrive are characterised by MAT 9 to 11 °C and 10 to 12 °C, WMMT 18 to 22 °C and 16 to 17 °C, CMMT –2 to 0 °C and 4 to 7 °C and MAP 700 mm and 700 to 1000 mm (Bohn et al. 2004) and match those inferred for Frankfurt/M using CLAMP.

A survey of climatic parameters of conifer taxa that are today absent from western Eurasia but persisted in East Asia and/or North America shows that most of these genera tolerate fairly low mean temperatures of the coldest month (Table 2). A single monotypic genus, *Glyptostrobus*, is currently restricted to areas with coldest month mean temperatures close to the freezing point. However, observations and experiments on freezing tolerance of modern conifers suggest that the realised niches in relict conifers are reflecting only a very small part of their fundamental niches (Sakai 1971; Bannister and Neuner 2001). Assuming a modern distribution of rainfall and temperature over the year (rain maxima in summer, coldest in winter), the modern climate of Lugano in the south of Switzerland would provide conditions to accommodate the Pliocene flora of Frankfurt (Fig. 21 a, c). In contrast, several

Table 4 New species described in the Pliocene flora of Frankfurt

Mädlar (1939) fruit and seed record	This study, leaf record
<i>Thuja pliocaenica</i>	<i>Magnolia waltheri</i>
<i>Potamogeton medicagoides</i>	<i>Pachysandra europaea</i>
<i>Carya longicarpa</i>	<i>Crataegus pentagynoides</i>
<i>Betula longisquamosa</i>	<i>Acer dombeyopsis</i>
<i>Corylopsis urselensis</i>	<i>Acer viburnoides</i>
<i>Eucommia europaea</i>	<i>Acer vitiforme</i>
<i>Prunus avifolius</i>	<i>Eucommia szaferei</i>
<i>Acer palaeo-miyabei</i>	<i>Populus gregorii</i> ^a
	<i>Populus canescentoides</i> ^a
	<i>Quercus praecastaneifolia</i> ^a

^a Described from the late Pliocene flora of Willershausen

suitable climates in humid warm temperate regions of south-western Europe and the eastern Black Sea region (Santander, Fig. 21b; San Sebastian, Batumi) have different rainfall and temperature patterns, with maximum rainfall in winter.

In a previous study, Thiel et al. (2012) used leaf physiognomic characteristics of dicotyledonous angiosperms (CLAMP, Spicer 2011–2019) to infer the palaeoclimate of Frankfurt. The reconstructed MAT (12.2 ± 1.2 °C), CMMT (2.3 ± 1.9 °C) and MAP (979–1333 mm) closely match the conditions in sheltered areas south of the Alps (see above Lugano, Ljubljana, Udine; Lieth 1999). It is noteworthy that highly similar climate estimates are obtained from modern climate envelopes of North American and East Asian conifers (Table 2) and from leaf physiognomic signal of broad-leaved angiosperm leaves.

Speciation and extinction in the late Pliocene of Europe

Many cool temperate northern hemispheric tree genera that were abundant during the Pliocene went extinct in Europe or became restricted to small relict areas in western Eurasia during the Pleistocene (Svenning 2003; Magri et al. 2017). For example, *Sciadopitys*, *Taxodiaceae*, *Tsuga*, *Carya*, *Pterocarya* and *Zelkova* persisted in northern Italy until less than one million years ago (Magri et al. 2017). The majority of taxa recorded for the Pliocene of Frankfurt persisted in western Eurasia until today (Table 1). According to Svenning (2003), increased cold and drought tolerance are important factors that determined whether tree taxa are still widespread in Europe, survived in relict areas or went extinct. Modern counterparts of extinct conifers in the Pliocene of Frankfurt are relatively cold tolerant (see above; Table 2) but are much more sensitive to cold than widespread modern cool temperate tree genera of Europe (cf. table 4 in Svenning 2003). Several new fossil species recognised in the present study and by Mäddler (1939) are noteworthy, as they might reflect a Pliocene radiation that did not persist into modern times. Mäddler (1939) established eight new species based on fruits and seeds (Table 3), while in the present study, seven new species were recognised (Table 4). Some of the taxa recognised as new species belong to genera that are still widespread in western Eurasia. For example, in the widespread northern hemispheric genus *Acer*, *Acer dombeyopsis* is morphologically closely similar to sections *Pentaphylla* and *Lithocarpa*, native to the Himalayas and East Asia. *Acer viburnoides* and *vitiforme* are extinct species in the Eurasian sect. *Acer*. *Acer* is still quite diverse in the flora of western Eurasia with ca. 17 species in three sections (van Gelderen et al. 1994; Grimm et al. 2007; Grimm and Denk 2014).

Likewise, the morphologically distinct *Quercus praecastaneifolia* strongly resembles a clade of East Asian white oaks (sect. *Quercus*) that is no longer represented in western Eurasia. It is interesting to note that leaf morphologies similar to extant East Asian species appeared in the Pliocene of Europe

but did not persist into modern times. The late Pliocene *Q. praecastaneifolia* appears to belong to a clade of modern white oaks restricted to the Himalayas to East and Northeast Asia that are relatively frost resistant. In this case, lack of frost and drought tolerance alone are not sufficient to explain why this species went extinct in Europe (cf. Table 2 and table 4 in Svenning 2003). Similarly, *Fagus* in Frankfurt is virtually identical to modern East Asian species (*F. hayatae* subsp. *pashanica*, *F. longipetiolata* and *F. crenata*) and has not much in common with the modern western Eurasian *Fagus* populations. Accepting a late Pliocene (ca. 3.6–2–6 Ma) age for the Pliocene flora of Frankfurt, it is interesting to note that a recent study placed the time of divergence of regional populations of *Fagus orientalis* from the remainder of *F. orientalis* and *F. sylvatica* in the early Pleistocene (1.18–1.87 Ma). *Fagus sylvatica* s.str. diverged from the remainder of western Eurasian *Fagus* populations at ca. 817 ka (Gömöry et al. 2018). This is in accordance with other studies (*Fagus*, Martinetto 2015; *Quercus*, Bagnoli et al. 2016; *Abies*, Piotti et al. 2017).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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